

ROOT-ZONE TEMPERATURE AND SOIL MOISTURE EFFECTS
ON GROWTH AND PHYSIOLOGY
OF CONTAINER-GROWN 'GRANDE NAIN' BANANA
AND IXORA CHINENSIS L. 'MAUI'

By

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BANANA AND IXORA CHINENSIS L. 'MAUI'

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Studies to investigate the effects of root-zone temperature (RZT) and irrigation volume (IRV) on growth and physiological responses of 'Grande Naine' banana (Musa spp. AAA) plantlets and Ixora chinensis L. 'Maui' were conducted under greenhouse (GH) and growth room (GR) environments.

Leaf photosynthesis (PS), conductance (CS) and transpiration (TR) in the GH were reduced 65%, 57% and 49%, respectively, in banana under an IRV of 20₊₄ ml daily per 150 cm³ container as compared with the highest IRV of 40₊₈ ml daily per container. Measured parameters were severely reduced at an IRV of 10₊₂ ml per container. Physiological responses of ixora were also reduced by decreased IRV. Leaf wilting occurred at a leaf water potential (LWP) of -1.1 MPa and leaves abscised below a LWP of -2.1 MPa.

In an RZT study, maximum midday PS in banana occurred at the 33°C RZT in a GH and a maximum midday PS of 0.74 mg CO₂ m⁻² s⁻¹ was observed in 33° and 38°C RZT-treated plants in a GR. In ixora, a 33°C RZT induced a maximum midday PS in the GH but there were no apparent differences in PS between 28°, 33° and 38°C RZTs in the GR study.

Maximum PS in banana occurred at 38° and 33°C RZTs under a higher IRV of 100₊₁₀ ml daily in the GH. In the GR, maximum PS occurred in 33°C RZT-treated plants and the higher IRV but at 38°C RZT under a moderate IRV (75₊₈ ml daily). Increasing RZT reduced leaf area under both IRVs. Carbohydrate (CHO) partitioning between shoot and root was correlated with RZT-induced changes in LWP.

Gas exchange processes in ixora were reduced by RZTs above 33°C RZT regardless of IRV. RZT-induced shoot growth was not associated with increased PS or TR but a hormonal role was theorized. CHO partitioning was likely related to the induced shoot growth and was influenced by environmental conditions.

These findings could have significant applications to banana production schemes using tissue-cultured plants. RZTs above 33°C could reduce the landscape and floricultural value of container-grown ixora.

CHAPTER I

GENERAL INTRODUCTION

Temperature and water are perhaps two of the most important environmental factors affecting growth and physiology of plants. Although soil moisture can be modified by irrigation, altering temperature is more difficult. Extreme temperatures produce deleterious but often subtle effects. Soil temperature and water are interrelated since both directly affect plant roots. Maintaining optimum water relations and temperature may be difficult, especially with container-grown species.

Hot and dry conditions often occur simultaneously in crop situations and alleviating the latter is often considered a remedy for the former. Although many drought tolerant plants are heat tolerant (85), the interactions between temperature and water stresses have not been well defined (102). Suboptimal root-zone temperatures (RZT) stress plants through reduced respiration, increased water viscosity (82) and reduced absorption caused by decreased cell membrane permeability (74). In this context, increased RZTs, within limits, are believed to have the reverse effect and so increase water (5,30) and possibly nutrient absorption (39,44).

Within limits, increased soil temperatures have generally increased shoot growth curvilinearly (30). Restricted shoot or leaf elongation is usually the first symptom of mild water stress (57). Reduced soil water might offset increased shoot growth induced by increasing soil temperature to within the optimum range. A similar induction of increased nutrient absorption by increasing soil temperature may occur thus permitting less than normal nutrient application. Such a recommendation was made for peppers (Capsicum annuum L.) grown at a supraoptimal RZT of 36°C (44).

Water stress, by its immediate effect on shoot growth but delayed action on photosynthesis (13), has been shown to increase shoot carbohydrate concentrations (8,119). Increased root temperature has also been shown to reduce shoot carbohydrates (7), again suggesting the possibility of interactive effects between the two stress factors. Indeed some pasture grasses were of better quality because of higher carbohydrate levels under high temperature and dry conditions as opposed to being irrigated (18).

Interactive effects of soil water and RZT on translocation and carbohydrate partitioning patterns have been reported (7,8). Increased RZTs have altered translocation rates due to increased sink demands of roots (46). Water stress could reduce translocation by its effect on reduced turgor pressure and the consequent effect on decreased mass flow of assimilates.

Therefore, the overall objective of this study was to identify the effects of supraoptimal RZT and water deficits on two container-grown plants. The specific objectives were to

1) Determine growth and physiological effects on 'Grande Naine' banana (Musa spp. AAA) and ixora (Ixora chinensis L. 'Maui') and to elucidate whether the two stress factors act independently or interactively.

2) Identify any compensatory type interactions that may be exploited in container production of plants.

3) Determine if drought stress can be induced by high RZT, identify critical RZTs and observe whether watering offsets temperature-induced water stresses.

Banana and ixora were selected because they represent a contrast in morphology, phenotype and horticultural usage. The use of tissue-cultured banana plants in this study represents a unique application of micropropagation as a tool in plant physiology. The choice of banana was also in anticipation of the stress problems that may arise in the banana production schemes that convert to the use of tissue-cultured plantlets.

CHAPTER II

LITERATURE REVIEW

Introduction

Temperature and water stress affect plant growth and physiological processes. The literature is abundant with data describing their independent effects but there have been few attempts to separate the effects of these two stress factors when applied in combination. Any attempt to determine interactions between soil water and temperature on plants must first review or determine their independent effects.

While it is generally accepted that water stress reduces expansive growth and induces a progressive reduction in gas exchange processes, the effects of supraoptimal RZTs have not been clearly identified. Soil water deficits usually reduce plant water status and supraoptimal RZTs may affect root absorption and conductance and indirectly stomatal function. However, plant water stress can occur even with adequate soil water when ambient conditions favor excessive transpiration or water absorption is inhibited by factors including high RZT.

Since supraoptimal root temperature directly affects root respiration and metabolism, its effect on partitioning

patterns within the plant seems likely more direct than that of water stress.

Water stress physiology

Water stress basically results from an imbalance between soil water absorption and that required by plants to meet transpirational needs. Kramer (74) stated that plant water stress is caused by either excessive water loss, inadequate absorption or a combination of the two. In general, an increase in water stress produces a two phase response in photosynthesis, with a threshold water potential above which there is little or no change in photosynthesis and below which the rate decreases rapidly (114). A water potential of -0.4 MPa reduced the photosynthetic capacity of loblolly pine with assimilation being negligible at -1.1 MPa (17). This effect was caused by stomatal closure which reduced transpiration as well as photosynthesis. Water stress may affect photosynthesis via three major mechanisms (131): 1) by stomatal closure, 2) by cellular dehydration which reduces enzyme activity, and 3) by decreasing cell membrane permeability to carbon dioxide and bicarbonate.

Although stomatal closure has been cited as the primary method by which water stress affects photosynthesis (13,78,132), there are several reports of non-stomatal reductions in photosynthesis (14,23,49,114). Many species that exert some degree of stomatal limitation on photosynthesis at low water potentials characteristically have high mesophyll resistance (50,141). When the components

of leaf resistance to CO_2 were measured for several species, mesophyll resistance was found to be lower than stomatal resistance but about ten times that of boundary layer resistance (139). Soil water deficit also affects the diurnal pattern of stomatal aperture (33) with progressively earlier closing under prolonged drought conditions (93).

Stomatal closure affected photosynthesis mainly by its effect on the carbon dioxide supply (13,17). However, some researchers agree that photosynthesis is evident even when stomata are closed (93). Because of their diffusive nature, photosynthesis and transpiration are both affected by stomatal closure, although transpiration may be affected more than photosynthesis (48,120). Photosynthesis was reduced 25% while transpiration decreased 50% in apple (Malus pumila Mill.) under drought conditions (51). Zelitch (149) indicated that partial stomatal closure reduced transpiration relatively more than photosynthesis. Although the diffusive resistance of CO_2 was larger than that of water, CO_2 also encountered a vastly greater mesophyll resistance than water. Consequently, the stomata represented a smaller portion of the total resistance to CO_2 than to water vapor.

Moorby et al. (95) found no effect of drought on the activity of ribulose 1,5-diphosphate (RUDP) carboxylase or carbonate dehydratase, two enzymes involved in CO_2 fixation. Ackerson et al. (1) however, reported that water stress reduced the activity of photosynthetic enzymes of potato (Solanum tuberosum L). Lawlor (84) indicated that ATP

synthesis through photophosphorylation was inhibited by water stress while electron transport and reductant supply were relatively insensitive. Boyer (14) demonstrated that photosynthesis of water stressed sunflower (Helianthus annuus L.) plants under growth chamber conditions was affected more by photochemical activity than by CO₂ diffusion or enzymatic activity. Davies (33) showed that stomatal sensitivity to decreasing leaf water potential in cotton (Gossypium hirsutum L.) and soybean (Glycine max. L.) was greater for plants grown in a growth chamber than in a greenhouse.

When soil moisture is adequate, diurnal fluctuations in xylem pressure potential closely followed the daily trend of atmospheric evaporative demand, whether expressed as radiation, vapor pressure or humidity (22,71,121). As soil moisture becomes limiting, early morning leaf water potentials (LWP) begin at a lower value, decrease sharply and then remain constant over several hours, reflecting the influence of increased stomatal resistance (29,108). Threshold relationships between diffusive resistance and leaf water potential appear to be more common than linear or curvilinear relationships (52,67,68). Brix (17) showed that net assimilation rate (NAR) was closely related to LWP; NAR began to decrease at -1.0 MPa and completely ceased at -3.5 MPa. Other reports (53,79,113) indicated that parallel decreases in NAR and LWP were strongly linked to changes in diffusive resistance. However, NAR changes in pear (Pyrus communis L.) (77), Pacific silver fir (Abies alba Mill.) and

noble fir (Abies nobilis Lindl.) (55) did not always coincide with changes in diffusive resistance indicating the influence of mesophyll and or carboxylation resistance. It was concluded that species vary considerably in their physiological reactions to water deficits.

The majority of studies on water stress in banana have dealt primarily with the effects on fruit bunch and yield characteristics, but with few details reported on morphological, phenological and physiological responses. However, all reports agree that water stress causes a general reduction in growth (19,111,136). Daniells (31) in Australia indicated a dramatic reduction in growth, delayed bunch emergence, inferior fruits and longer maturity time for 'Williams' banana under decreasing soil water levels. Robinson and Albertson (116) reported that optimum growth and yields were obtained by maintaining soil moisture levels at 16 to 34% of total available soil moisture (ASM). Bhattacharyya and Rao (10) also reported optimum bunch and yield characteristics with 20 to 40% ASM depletion levels. An unimpeded supply of water was essential for development of an efficient root system, rapid rate of leaf emergence, continued production and partitioning of assimilates, and synthesis of growth hormones such as cytokinins. In Honduras, Ghavami (40) found an irrigation rate of 44 mm/week or a soil moisture tension of 30 to 40 centibars resulted in the highest yields of 'Valery' banana.

Perhaps the most detailed description of the effects of soil water levels on banana physiology was recorded by Shmueli (126) in his paper on the physiological activity of banana in relation to soil moisture in Israel. Depletion of soil moisture below a third of the available water capacity was accompanied by marked yellowing of leaves and significant reduction in stem diameter. Diurnal changes in stomatal activity were clearly related to ASM. When soil moisture decreased below two-thirds of total ASM, there was a reduction in stomatal conductance which was confined mainly to the morning hours. The impairment of plant water balance became acute when soil moisture decreased to about one-third of the total available. Although diurnal patterns of stomatal conductance and transpiration generally paralleled each other, the rate of transpiration was considerably more influenced by environmental conditions. Soil moisture levels below two-thirds of field capacity resulted in reduced leaf osmotic potential. Overall, banana plants responded to diminishing soil moisture by stomatal closure, reduced assimilation and accelerated yellowing of leaves indicative of starvation effects.

Current efforts to increase agricultural production, coupled with conservation of limited high quality water, have focused attention on the possibility of increasing water use efficiency (WUE) of various crops (16,88,97). Fischer and Turner (38) observed that under field conditions, WUE usually remained constant or increased slightly with increasing soil

water limitations for C_3 species. Reports on the effects of water stress on WUE are conflicting. Some investigations pointed to only small increases in WUE with water stress (16,38,97). Reduction of water supply to wheat (Triticum aestivum L.) such that transpiration was reduced by 70% of the controls was associated with a 20% increase in WUE (41). On the other hand, WUE in maize (Zea mays L.) was lower on days when there was increasing soil water stress (128). Limited soil water resulted in yield losses but enhanced WUE in grapefruit (Citrus paradisi L.) (16) and Shamouti orange (Citrus sinensis Osb.) (97). Manning et al. (86) found a positive correlation of WUE with soil moisture regime, plant height, leaf area and seed yield in pea [Pisum sativum (L.) Mer.].

Adequate irrigation was critical for vegetative growth in coffee (Coffea arabica L.) (4,72) and water stress reduced extension growth, node number and leaf area (138). Ten and 25 ml water/day/coffee seedling in 15 cm pots resulted in drastic growth reduction, wilting and necrosis of the terminal shoots compared to a 200 ml treatment which caused water logging and induced leaf abscission (72).

Water stress has been shown to cause specific changes in plant carbohydrate status. Decreased starch concentration simultaneous with increased sugar content during drought stress have been reported for sugar maple (Acer saccharum Marsh.) (106) and black oak (Quercus velutina Lam.) (107). In sugar maple total carbohydrates were not affected, indicating

a change in carbohydrate partitioning. Similar changes in carbohydrates occurred in the inner bark of loblolly pine (Pinus taeda L.) (56) and in cotton shoots (36). Water stress induced increases in sugar concentration may serve several purposes, of which two are of major significance. Increased sugars increase the readily available substrate for respiration (17). A second effect of increased free sugars during water stress is to lower the osmotic potential of the cell solution and hence maintain cell turgor. Concentration and form of carbohydrates, organic acids or inorganic ions are modified to promote osmotic regulation (74). A more negative leaf solute potential with water stress was observed in seedlings of English oak (Quercus robur L.) and silver birch (Betula pendula Rodt.) but the degree of osmotic regulation varied between species (105).

Munns and Pearson (98) found that reduced photosynthesis as a result of water stress was not caused by accumulation of photosynthates in potato leaves. Low leaf water potential resulted in decreased translocation of carbohydrate, which was proportional to the decline in net photosynthesis, irrespective of whether tubers were present. A lower proportion of labelled $^{14}\text{C}\text{O}_2$ was found in tubers of stressed potato plants compared to non-stressed plants (125).

One of the earliest plant responses to water stress is reduced elongation of leaves, stems and roots (57). Boyer (13) found that leaf enlargement of corn and soybean

was inhibited earlier and more severely than photosynthesis and respiration by decreasing water potentials.

Physiological Effects of Root-Zone Temperature

According to Levitt (85) the two major forms of stress injury are direct and indirect injury. Direct heat injury results from a short exposure to an extreme temperature and is detectable immediately at the cellular level. Indirect injury results from prolonged exposure to temperatures below those causing direct injury.

Supraoptimal temperature stress may be defined as the retardation or cessation of metabolic functions in response to high temperatures. Alexandrov (3) reported that the first symptom of high temperature was the cessation of protoplasmic streaming. This was followed by a reduction in photosynthesis with subsequent damage to the chloroplasts. Finally, semipermeability of cell membranes was disrupted, so that cellular compartmentalization was lost with mixing of cellular contents.

Starvation, a common form of indirect heat injury in plants, occurs because of a higher optimum temperature for respiration than photosynthesis (85). The temperature at which photosynthesis and respiration rates are equal is the temperature compensation point. When plant temperatures exceed this critical point, carbohydrate reserves become depleted and starvation ensues. Other forms of indirect metabolic injury (85) are toxicities resulting from

disturbance of specific metabolic processes and biochemical lesions resulting from the accumulation of metabolites necessary for plant growth.

Ingram and Buchanan (61,62) demonstrated that electrolyte leakage through root cell membranes in response to increasing supraoptimal temperatures was sigmoidal and the midpoint of this response was defined as the critical temperature. Critical temperature was species and cultivar specific and varied from 48° to 53°C for a 20 minute exposure time (61,62). Direct injury at high temperature was also shown to be a function of exposure time (60).

Proteins are denatured by high temperature (2) and there is evidence that high temperature disrupts membrane structure. Inhibition of photosynthesis at high temperature was correlated with the disruption of membrane associated-processes including photosystem II (108), photophosphorylation (123) and the change of chlorophyll organization (122). The stability of membranes is mainly due to the degree of fatty acid saturation which is linked to membrane function and organelle association (145). Environmental temperatures have been demonstrated to alter fatty acid saturation ratios and membrane fluidity as adaptive responses to high and low temperatures (24,27,28,45,87).

There are several reports of the effects of growth medium temperature on water uptake by roots (70,89,104,115). Water conductivity through roots appears to be a temperature-

dependent process (117). Low temperature reduced transpiration and stomatal conductance in chill-susceptible species by reducing conductance through root cell membranes (75,104,147). Such results are most likely due to increased resistance to water at the endodermis layer (89).

Heating the root-zone to temperatures within the optimum range generally improved plant growth (12,42,83) and heating the root medium to 20°C improved foliage plant production at low greenhouse air temperatures (12). Root temperatures above or below optimum may alter hydraulic conductivity and thus indirectly affect stomatal conductance, photosynthesis and subsequent carbohydrate translocation (66). Optimal root-zone temperature in tomato (Lycopersicon esculentum Mill.) ranged from 30° to 36°C for nutrient translocation and water absorption (42,58).

Using plants with heat-killed roots, Kramer (73) showed that plant shoots remained alive and did not wilt for several days even after root death. Transpiration decreased after root death because of leaf injury and gum deposits from dead cells. Citrus hydraulic root conductance increased linearly with increasing root temperature (137) and Carrizo citrange exhibited a log-linear decrease in conductivity over a temperature range from 40° to 10°C (146).

Cooper (30) published an extensive literature review in 1973 on RZT effects and reported important differences due not only to species and cultivars but also to growing conditions. High leaf photosynthetic rates in soybean grown

at increasing RZT were related to low stomatal resistance, high transpiration rate and high phosphoenol pyruvate and RUDP carboxylase content (35). Cucumber (Cucumis sativus L.) leaves were larger, contained more chlorophyll and produced greater amounts of ATP and NADPH when plants were grown at 25°C RZT compared to 15° or 35°C (26). Canopy photosynthesis of pepper plants was closely related to shoot dry weight and crop yield (44), although maximum growth and yields were obtained at 30°C RZT and maximum photosynthesis rates were recorded at 36°C RZT. The disparity between optimal RZTs was explained by increased rates of respiration at the higher RZT. High rates of photosynthesis at high RZT in tomato were due not only to increased plant size but also to a modification of the physiological and morphological properties of the photosynthetic apparatus (43). Chlorophyll content (26), enzyme activity (35) and leaf hormonal content (91) have been influenced by increasing RZT.

Although many physiological processes are influenced by high RZTs (30), there is relatively little information on the effects of RZT on endogenous hormone levels (76). High RZTs have been reported to increase gibberellin and decrease cytokinin translocated in the root exudates (47,64,129). There is also evidence that high RZT may affect the distribution of gibberellin in the shoot (76). Alternatively, high RZT may have increased the activity in the roots of gibberellins previously synthesized in the shoot as well as influenced synthesis in the shoot (110).

In a study on flowering in coffee (92), ambient temperatures above 33°C induced formation of orthotropic shoots and prevented flower initiation. Root-zone heating delayed flowering and induced excessive vegetative growth in peppers (44). Such an antagonism between vegetative and reproductive growth prompted the authors to recommend a reduction in night temperature or nitrogen fertilization when pepper plants are grown at high RZTs.

Reduced biosynthesis of cytokinins induced by supraoptimal RZT was thought to reduce photosynthetic rates in bean (Phaseolus vulgaris L.) (21) and grape (Vitis vinifera L.) (129). Increasing RZTs from 18° to 30°C in rice (Oryza sativa L.) increased the translocation and rate of photosynthetically assimilated ^{14}C into the roots but decreased root growth apparently by retarding protein and cell wall synthesis (96).

Temperature has long been recognized as the main environmental determinant of plant growth and phenology (81). Increased soil temperatures have generally increased shoot growth curvilinearly and reduced root growth (30,112). All growth variables of Pittosporum tobira Thunb. were substantially lowered by a 40°C RZT for 6 hrs/day compared to 27°C (65), and Ingram (59) noted marked growth inhibition of woody plants stressed by 35° to 40°C RZT for 6 hrs/day.

Gosselin and Trudel (44) reported maximum leaf area in pepper at a RZT of 30°C with a decline at higher temperatures. Watts (144) demonstrated reduced leaf expansion

in maize with increasing RZT but could not explain this as a result of increased plant water deficits. RZTs above 37°C restricted leaf growth and rate of emergence in pearl millet (Pennisetum typhoides S&H) (103). Soil temperatures of 37°C and above, which are common in the tropics, reduced both root and shoot growth of maize and cowpea (Vigna unguiculata L.) (90). Well-watered potted eggplants (Solanum melongena L.) exhibited decreased plant growth with increasing RZT from 25°C to 40°C (118). Shoot to root ratio, however, was constant except at 40°C, where root rot occurred.

Philpotts (109) reported a linear decrease in cowpea nodulation and total plant dry weight with increasing RZT from 31°C to 40°C. RZTs above 32°C significantly reduced vegetative growth of two cultivars of cowpea through their effects on shoot, peduncle and root dry weight and, to a lesser extent, leaf number (94).

Using a system of circulating water coils, Franco (39) applied RZTs from 13°C to 48°C and observed the effects on coffee growth, transpiration and mineral absorption. Maximum transpiration occurred at 33°C with a significant decline at 43°C. Similarly, RZTs above 33°C reduced absorption of several nutrients and induced leaf chlorosis. Plants growing at 48°C died and both shoot and root growth were depressed above 33°C. In another experiment using young coffee seedlings grown at 33°C RZT, he reported the occurrence of small tumors at the base of the stem from which new orthotropic or non-flowering shoots grew.

In an extensive investigation using 'William' banana in sunlit growth chambers, Turner and Lahav (142) reported heat injury at an air temperature of 37°C. Total plant weight was greatest at 28°C while leaf area was maximum at 33°C. Temperature altered partitioning patterns in the whole plant and at 33°C more leaves and less stem and roots were produced, giving increased shoot to root ratios. Lamina leaf folding also occurred at high air temperatures and the authors implied that induced high vapor pressure deficits may have been the cause. Severe constraints on data measurements were imposed by the large nature of the banana plants and restricted growth chamber space. This could, in part, explain why critical physiological data such as photosynthesis, transpiration and leaf water potential were not recorded. Assimilate partitioning results were estimated using relative growth rate formulae and no analyses on tissue carbohydrate status were performed.

Root-Zone Temperature and Soil Moisture Interactions

The complexity of responses of RZT and soil moisture stress alone are such that few researchers have attempted studies on their interactive effects. Lal (80) reported in 1974 that a RZT of 35°C significantly decreased root and shoot growth and transpiration in maize seedlings. Effects of high RZT were aggravated by low soil moisture levels. Changes in soil water supply and RZT were found to have predictable

effects on the relationship between leaf water potential and transpiration rate in several tree species (37,54,68,135).

Kaufmann (69) evaluated the effects of RZT (6° to 20°C) and two soil drying cycles (9 and 12 day) on water relations and growth of Monterey pine (Pinus radiata. Don) under greenhouse conditions. The slope of the relationship of xylem pressure potential to transpiration was influenced by RZT. Under well-watered conditions, neither transpiration nor stomatal conductance were affected by RZT because xylem pressure potential was not low enough to cause stomatal closure. At the end of 9- and 12-day drying cycles, however, transpiration was lower than in the well-watered controls as a result of stomatal closure. RZT apparently had no consistent effect on transpiration rate. Reduced RZTs and soil drying both significantly reduced shoot and root extension after 28 days even though low RZT did not cause stomatal closure.

In an earlier study with 'Monterey' pine, Babalola et al. (5) measured photosynthesis, transpiration and respiration at four soil water levels and four RZTs (10° to 27°C). They found that the rates of photosynthesis, respiration and transpiration decreased with increasing soil water deficits. However, only at soil water levels lower than -0.7 bars and at RZTs of 10°C and above were the rates of photosynthesis and transpiration affected similar to changes in stomatal conductance.

Barlow et al. (7) studied the effects of RZT and soil water potential on corn seedlings. This investigation also did not involve supraoptimal temperatures but there were notable interactive effects. Rates of leaf elongation, net photosynthesis, transpiration and leaf water potential were simultaneously monitored under varying stress conditions. In their first study, leaf elongation was found to be much more sensitive to changes in root temperature (12° to 28°C) than either photosynthesis or transpiration and ceased at a LWP of -0.9 MPa; physiological responses were not affected until LWPs of -1.2 to -1.3 MPa were attained. A decrease in net photosynthesis coincided with an increase in stomatal and mesophyll resistance at low LWPs. The authors concluded by emphasizing the need for whole plant studies so that stress effects on photosynthesis, translocation and assimilate partitioning could be better analyzed.

Two root temperatures (21.1° and 26.6°C) and two soil water potentials (-0.35 and -2.50 bars) were employed in their second experiment (8). Leaf elongation and total dry matter were decreased 44% and 26%, respectively, soluble carbohydrates increased 42% , while rates of transpiration decreased 24% at the low soil water potential. There were also some interactions between RZT and soil water content. Dry weights for plants at 21.1°C and -0.35 bars were similar to those at 26.6°C and -2.50 bars. Higher soluble carbohydrate concentrations with increased water stress were offset by increased RZT. Decreased total plant dry weight and

transpiration at lower soil water levels were slightly offset by higher RZT, presumably through increased root conductance and water absorption.

Most of the studies involving soil temperature and moisture interactions on banana in the tropics have been field oriented and have involved the use of soil mulches which effectively reduce soil temperature and conserve soil moisture (10,11). In most cases, mulching led to increased WUE which was based on a yield to evapotranspiration ratio rather than on the physiological parameters of photosynthesis and transpiration. In the case of coffee, there are independent studies on soil temperature (39) and soil moisture (4,72,138), but no reports on their interactive effects.

CHAPTER III

EFFECTS OF IRRIGATION VOLUME ON BANANA AND IXORA UNDER TWO GROWING CONDITIONS

Introduction

Although 'Grande Naine' banana (Musa spp. AAA) is a mesophytic, herbaceous plant requiring moist soils for optimum production (127), it can be grown in marginal areas where soil water is limiting. Irrigation scheduled when available soil moisture depletion reaches 60% to 80% has been shown to be optimum (10,11,31,116), but detailed characterization of physiological responses in banana to decreasing soil water levels is lacking.

Moisture stress is thought to be necessary for flower induction (4) in coffee, a close relative of ixora (Ixora chinensis L. 'Maui') within the Rubiaceae family (6), but adequate irrigation (72) is essential for growth and mineral absorption (138). Because of its importance as a major beverage crop, there are several field (100,101) and container studies (39,72,138,140) on the physiological responses of coffee, but no work has been conducted on the effects of varying soil water levels on container-grown ixora. The present study investigated the physiological responses of banana and ixora to three irrigation levels and

a 14-day drying cycle. Irrigation experiments were conducted under both greenhouse and growth room conditions.

Materials and Methods

Plant Materials and General Cultural Procedures

Ten- to 12-cm tall tissue-cultured banana plants and similar-sized, uniform ixora rooted cuttings were obtained from commercial nurseries. Plants were hardened with intermittent mist (6 sec min^{-1}) in a glass greenhouse at 28°C under 80% light exclusion for one week, then moved to 40% light exclusion for another week. Plants were transplanted to white 4-cm diameter x 21-cm tall conical containers (150 cm^3) using Metro-Mix 300 growth medium (W.R. Grace and Co., Cambridge, MA). Plants were then moved to the experimental greenhouse or growth room where they were watered to container capacity daily and allowed to acclimatize for one week prior to the initiation of the experiment.

Greenhouse

Experiment 1. Experiment 1 was initiated in July, 1985, in an air-conditioned greenhouse in which maximum photosynthetic photon flux density (PPFD) ranged from 700 to $800 \text{ umol m}^{-2} \text{ s}^{-1}$, and temperatures were 25 to 30°C day and 18 to 21°C night. Relative humidity varied from 40 to 80% (Figure 3-1).

Plants were watered daily at 2200 hr with $10 \pm 2 \text{ ml}$ (W1), $20 \pm 4 \text{ ml}$ (W2) or $40 \pm 8 \text{ ml}$ (W3) per container. These irrigation

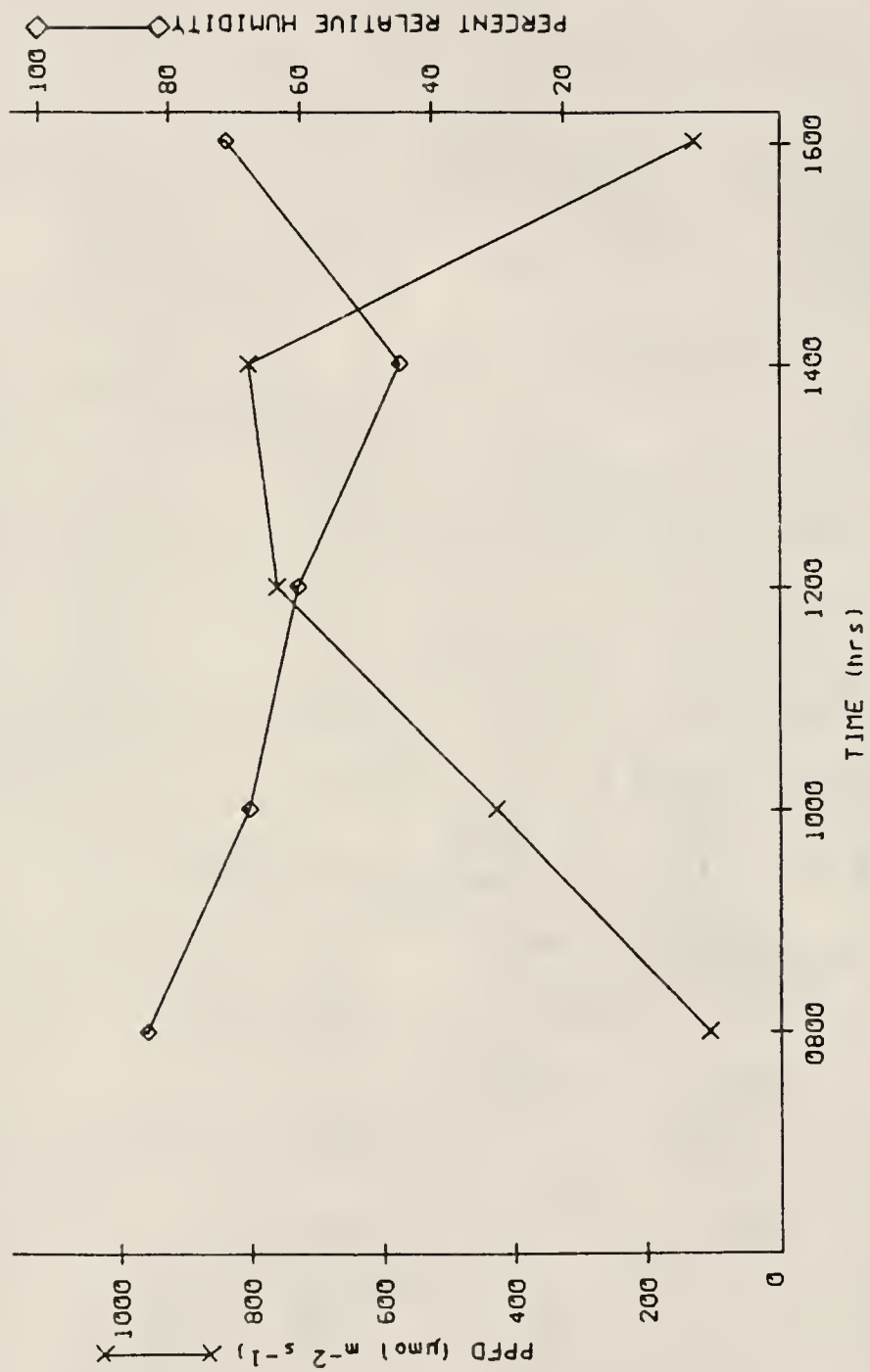


Figure 3-1. Photosynthetic photon flux density and relative humidity in the greenhouse during measurements of physiological parameters.

volumes provided 53% to 60%, 65% to 75%, and 85% to 100% container capacity (CC) respectively, for banana and 52% to 64%, 68% to 80% and 90% to 100% CC, respectively, for ixora. The comparatively smaller root mass of ixora was responsible for the difference in growth medium waterholding capacities between these plants. Water was applied automatically through drip tubes by a battery-operated controller (Water Watch Corp. Seattle, WA). One, two and four 1-mm drip tubes/container constituted the W1, W2 and W3 irrigation treatments, respectively.

After 14 days of irrigation treatments, diurnal measurements of leaf photosynthesis (PS), transpiration (TR) and leaf conductance (CS) were made using a portable photosynthesis system (Model LI-6000, LI-COR, Inc., Lincoln, NE). Measurements were initiated at 0800 hr EDT on a cloudless day and taken every 2 hr until 1600 hr. A 1-liter cuvette chamber was used for measurements and the mean of eight consecutive 30-sec observations on each leaf constituted a measurement. A zero check of the analyzer was performed between treatments within each replicate. Simultaneous measurements of LWP were made using a Scholander type pressure chamber (PMS Instrument Model 600, Santa Barbara, CA) as described by Barrett and Nell (9). The third most recently expanded leaf in banana was selected for measurements of both gas exchange and LWP. This leaf has been shown to be the most responsive and the youngest with fully developed stomata (127). Gas exchange processes in ixora were

measured on the most recently matured leaves but apical shoots were sampled for LWP. Six plants per treatment were sampled for all measurements.

Experimental design was a randomized complete block with 21 plants per water treatment within each of three blocks. Six replicate plants were randomly selected at each sampling time. Water use efficiency (WUE) was calculated from PS/TR. Means and standard errors were calculated and plotted against time of day.

Experiment 2. In order to further monitor physiological responses of water stress and correlate these with visual plant symptoms, water was withheld from banana and ixora plants for 14 days beginning one week after transplanting. This drying cycle study was conducted simultaneously with experiment 1 in the same greenhouse and similar cultural practices were used. Midday LWP and CS measurements were recorded on five plants of each species at 2-day intervals using the procedures described in experiment 1. A completely randomized design was used in this experiment and means and standard errors were calculated. There were five replicate plants per treatment for each sampling date.

Growth room.

Experiment 3. Experiment 1 was repeated in a 3.0 m by 7.6 m walk-in growth room in order to investigate physiological responses to water stress under more precisely controlled environmental conditions. Irradiance of $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, as measured by a quantum radiometer (LI-COR

Model LI-185A, LI-COR Inc., Lincoln, NE), was supplied at plant canopy level by 1000 W phosphor-coated metal-arc HID bulbs (GTE Sylvania Corp., Manchester NH) from 0600 to 1830 hr daily. Air temperatures of 28°C day and 21°C night and a relative humidity of 65% to 70% were maintained. Three irrigation volume treatments were applied as in experiment 1 in a randomized complete block design with three blocks and 21 plants per water treatment per block. Species were treated and analyzed as separate experiments. On the fifteenth day after water stress treatments, diurnal measurements were initiated at 0800 hr and continued at 2-hr intervals until 1800 hr. Leaf sampling methods and measurement procedures for PS, CS, TR and LWP were employed as in experiment 1.

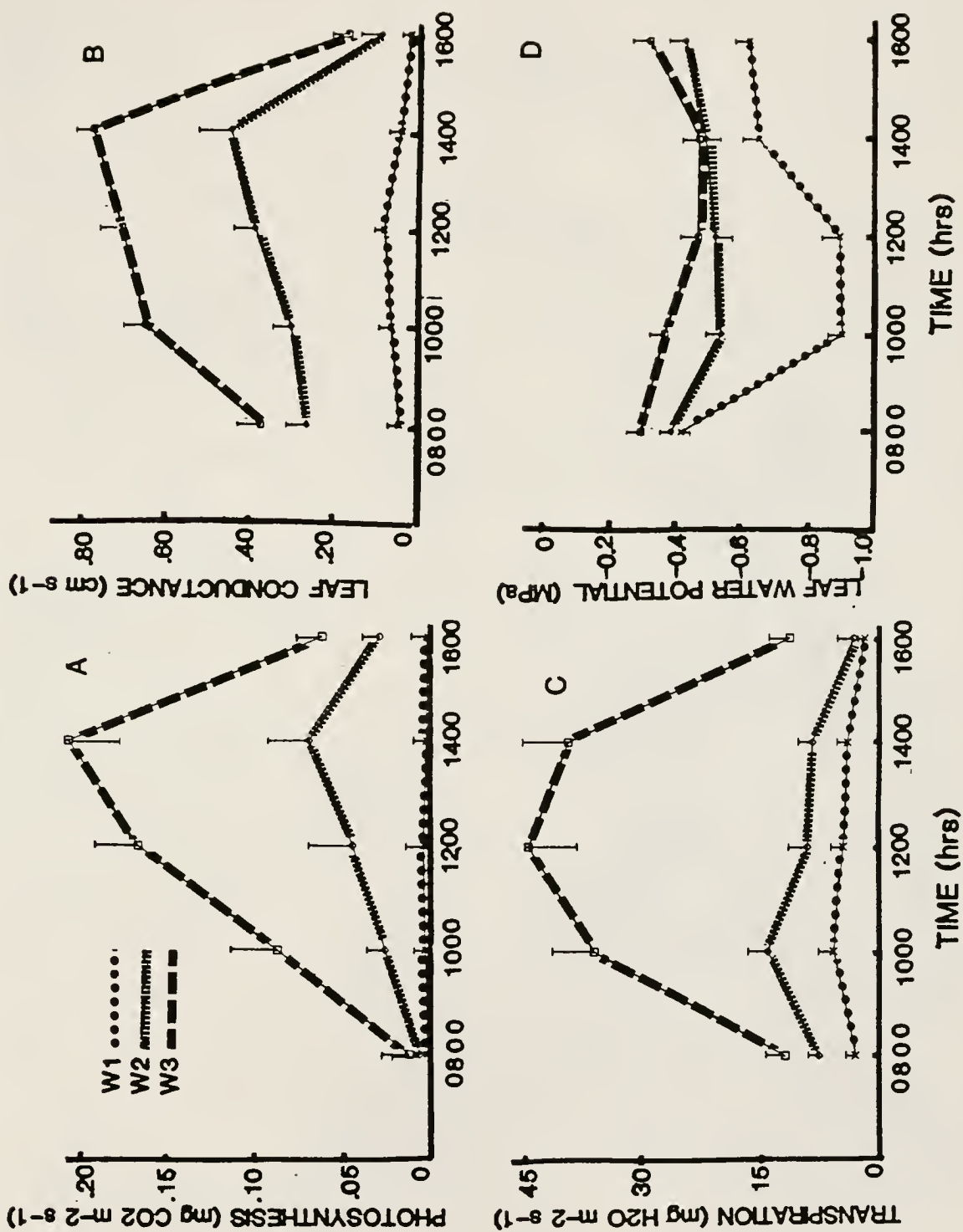
Results and Discussion

Greenhouse

Experiment 1--banana. Irrigation treatments influenced daily PS, CS and TR maxima as well as diurnal patterns (Figure 3-2A, 3-2B, 3-2C). Relatively high LWP were maintained by plants in the W2 and W3 irrigation treatments but there was a distinct decline in LWP by 1000 hr in plants receiving the lowest irrigation volume, W1 (Figure 3-2D).

PS patterns of plants under the W3 and W2 irrigation treatments paralleled the corresponding CS patterns, with a rise in PS from 0800 hr to a peak at 1400 hr of 0.20 mg CO₂ m⁻² s⁻¹ for the W3 treated plants. Maximum PS for plants in the W2 irrigation treatment were reduced almost three-fold

Figure 3-2. Effects of three irrigation volumes on the diurnal physiological responses of 'Grande Naine' banana grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. W1 = 10+2 ml, W2 = 20+4 ml and W3 = 40+8 ml daily per 150 cm³ container. Points are the means of six replicate plants and vertical bars represent the SE.



below plants at W3 (Figure 3-2A). PS for the W1 treated plants was significantly reduced compared to plants in the other irrigation treatments with a midday rate of only $0.003 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

CS in plants receiving the highest irrigation volume, W3, averaged 0.37 cm s^{-1} at 0800 hr, had more than doubled by 1400 hr and declined sharply to 0.17 cm s^{-1} at 1600 hr (Figure 3-2B). CS in plants under the W2 irrigation followed the same pattern, but was reduced by 50%, 47% and 49% at 1000, 1200 and 1400 hr, respectively. CS in plants at the lowest irrigation level did not change appreciably throughout the day and averaged only 0.08 cm s^{-1} , suggesting that the stomata remained nearly closed throughout the day. Therefore, PS and CS were severely reduced by decreased irrigation and both declined in parallel.

Although TR increased from 0800 hr to 1000 hr for both W2 and W3 treated plants, TR in W2 and W1 plants was significantly lower (Figure 3-2C). TR remained somewhat stable between 1000 and 1400 hr for all treatments and declined significantly between 1400 and 1600 hr under the W3 irrigation volume. Maximum TR was 44.4, 14.2 and $6.3 \text{ mg H}_2\text{O m}^{-2} \text{ s}^{-1}$ for the W3, W2 and W1 treated plants, respectively.

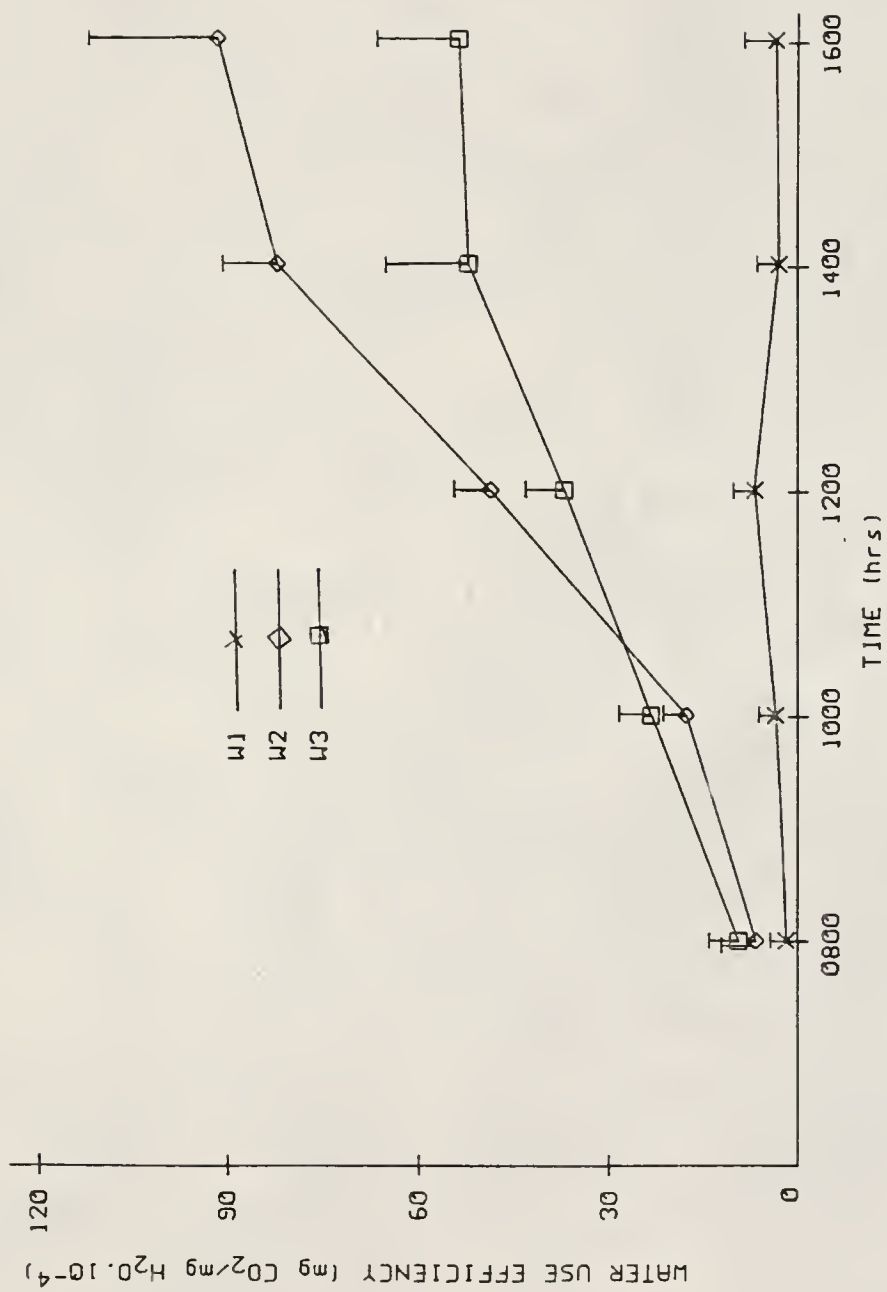
LWP of plants under the W2 and W3 irrigation treatments were fairly stable throughout the day, but LWP of plants at the lowest irrigation level declined significantly after 0800 hr to a low LWP of -0.90 MPa at 1000 and 1200 hr (Figure 3-2D). Although there was an increase in LWP for W1 treated

plants after midday, the LWP at 1600 hr of -0.62 MPa remained significantly lower than the 0800 hr LWP. The reduction in CS and the decline in gas exchange processes but not leaf water status at midday and 1400 hr for the W2 treated plants, indicated that there were factors other than leaf water status controlling stomatal opening.

Water use efficiency (WUE) for plants under the W3 and W2 irrigation levels increased almost linearly throughout the day but did not differ between treatments until 1200 hr, after which WUE in W2 treated plants was higher (Figure 3-3). This indicated that TR in plants under the W2 treatment was reduced more relative to PS. However, the WUE pattern for the severely stressed W1 treated plants remained low throughout the day. The leaf folding mechanism commonly observed in field-grown banana plants at midday hours (127,136) was observed in the W2 treated plants. Increased WUE values, though calculated on a yield/evapotranspiration ratio, have also been obtained for field-grown bananas under moderate reductions in soil moisture levels (11).

Altered physiological processes in banana with decreasing irrigation levels agrees with Shmueli's work (126) in which TR and CS in Cavendish banana were reduced by available soil moisture levels below 66%. Chen (25) also found a similar effect at a soil water level of 50% to 60% field capacity. These were both field studies in which soil moisture effects could have been confounded by ambient vapor

Figure 3-3. Effects of three irrigation volumes on the diurnal water use efficiency of 'Grande Naine' banana grown under greenhouse conditions. W1 = 10+2 ml, W2 = 20+4 ml and W3 = 40+8 ml daily per 150 cm³ container. Points are the means of six replicate plants and vertical bars represent the SE.

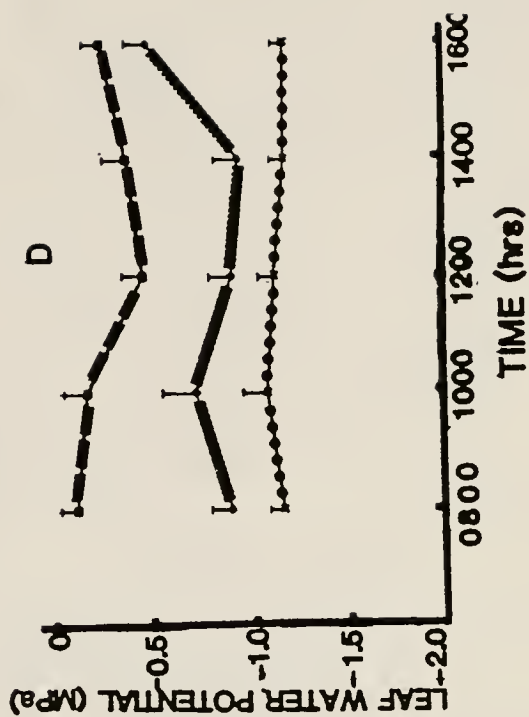
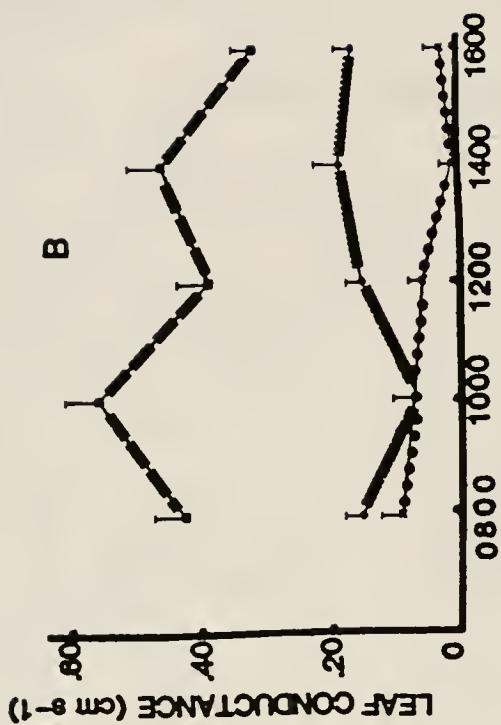
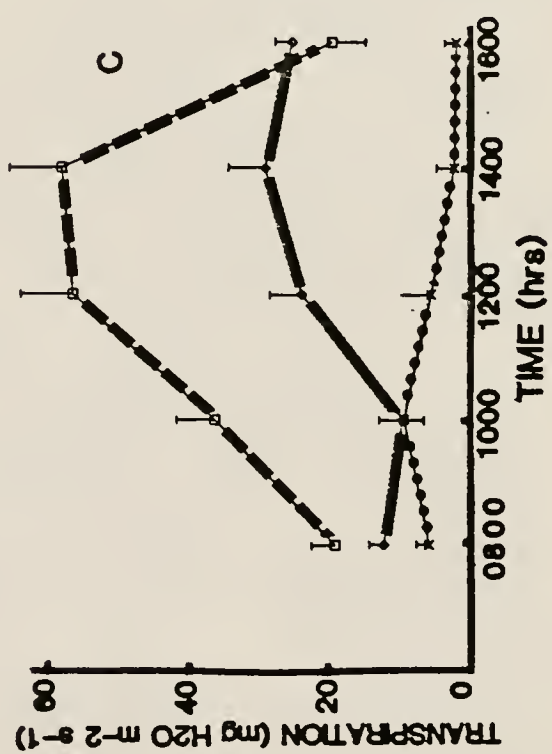
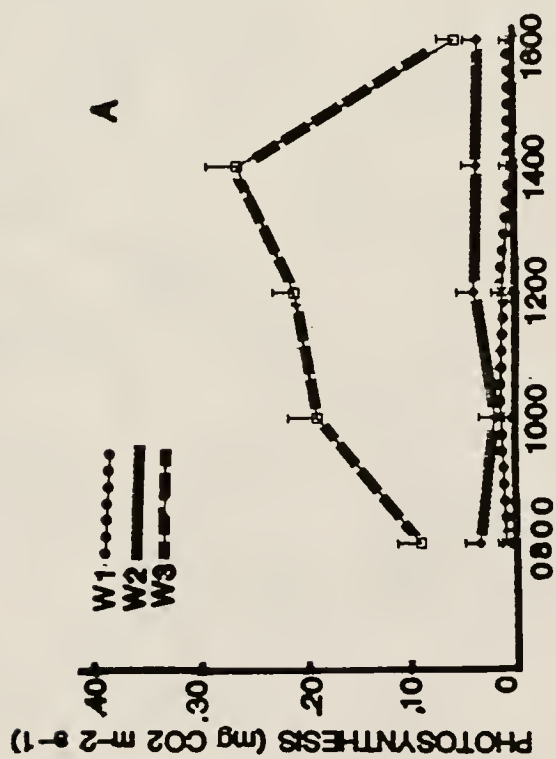


pressure deficits to a greater extent than occurred in the present greenhouse experiment. CS and TR reported for both field studies, however, were closely correlated. Brun (20) reported good correlation between PS and TR in intact banana leaves in response to light intensity but CS was not monitored in his study. Results in the present experiment indicate that stomatal closure was associated with reductions in PS and TR.

Severe growth reduction and leaf chlorosis have been induced by soil moisture depletion levels below 50% in field studies (126). These effects were generally attributed to reductions in PS, although PS rates were not measured. The present study substantiates these hypotheses, since the lowest irrigation level produced similar water stress symptoms and significantly decreased PS (Figure 3-2A).

Experiment 1--ixora. Although irrigation treatments highly influenced measured parameters, diurnal patterns did not necessarily parallel one another (Figure 3-4). Under the W3 irrigation treatment, maximum PS and TR rates of $0.26 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $58.1 \text{ mg H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively, occurred at 1400 hr (Figure 3-4A, 3-4C). However, CS was somewhat erratic, with a maximum at 1000 hr, followed by a decline at 1200 hr and a small rise at 1400 hr (Figure 3-4B). PS and CS were significantly reduced by the W2 and W1 irrigation levels through 1400 hr compared to W3 and under the W1 level CS and TR appeared to be more closely related.

Figure 3-4. Effects of three irrigation volumes on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under greenhouse conditions. A. leaf photosynthesis \bar{B} . leaf conductance C. transpiration and D. leaf water potential. $W1 = 10 \pm 2$ ml, $W2 = 20 \pm 4$ ml and $W3 = 40 \pm 8$ ml daily per 150 cm³ container. Points are the means of six replicate plants and vertical bars represent the SE.



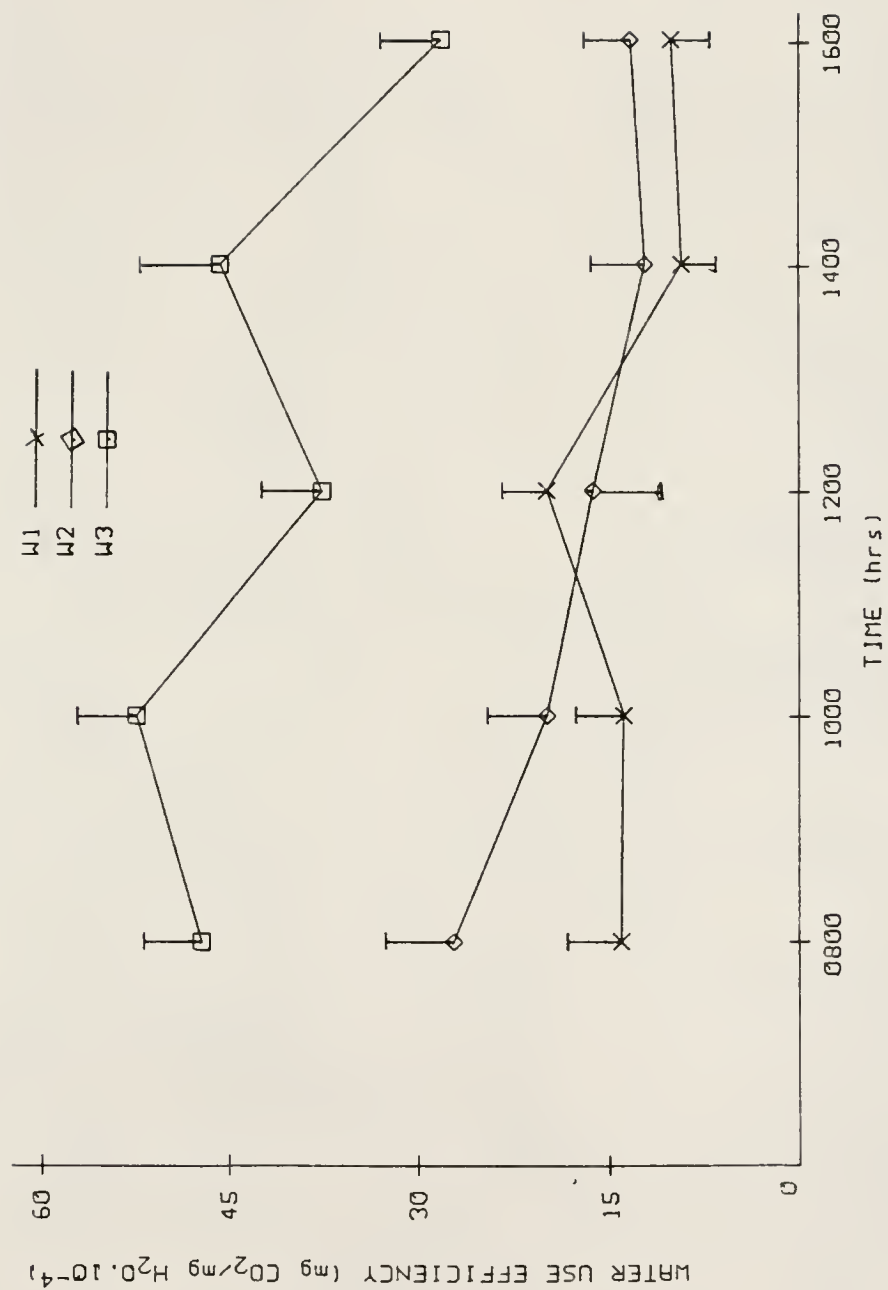
LWP was generally reduced by decreasing irrigation volumes (Figure 3-4D). Midday LWP for the W2 and W1 treatments were 2 and 2.5 times less than for plants under the W3 irrigation treatment, respectively. Irrigation treatments, therefore, were well distinguished by measuring LWP.

Reduced irrigation, however, decreased PS relatively more than TR as reflected in the higher WUE in plants at the W3 irrigation level compared to plants under the W2 and W1 levels (Figure 3-5). Non-stomatal inhibition of PS under water stress conditions have also been reported in other species (14,15) and may have contributed to the lower WUE observed with water stress in this study.

Although midday declines in CS have been noted for coffee (100,101,140) under well-watered field conditions, the suggestion that light was responsible (101) would not seem to apply to ixora. In the high light environment of the growth room CS did not decline at midday (Figure 3-10B).

A high irrigation treatment of 200 ml/15 cm pot/day induced flooding effects and caused leaf abscission in coffee (72). Such effects were not induced in this study by the highest irrigation treatment, W3, but the erratic midday stomatal response referred to above might have been in response to the high watering level.

Figure 3-5. Effects of three irrigation volumes on the diurnal water use efficiency of *Ixora chinensis* L. 'Maui' grown under greenhouse conditions. $W1 = 10+2 \text{ ml}$, $W2 = 20+4 \text{ ml}$ and $W3 = 40+8 \text{ ml}$ daily per 150 cm^3 container. Points are the means of six replicate plants and vertical bars represent S.E.



Experiment 2--banana. LWP decreased linearly while CS decreased in a sigmoidal pattern during the 14 days without irrigation (Figure 3-6). Leaf folding along the midrib is a common feature of water-stressed field-grown banana plants at midday hours (127,136), but plant water status associated with the mechanism has not been previously defined. In this study, leaf folding occurred between day 4 and 6 and coincided with a decline in LWP from -0.51 to -0.65 MPa and a decrease in CS from 0.46 cm s^{-1} on day 4 to 0.051 cm s^{-1} on day 6. In experiment 1, leaf folding was also observed in the W2 treated plants at midday with comparable LWP and CS. This response therefore, substantiated the irrigation-volume method as a fairly accurate, practical means of imposing water stress treatments in banana. Anatomical studies have indicated a special band of cells along the midrib of the banana leaf (130) which are responsible for the folding response and it is likely that these cells are more responsive to decreasing LWP than the other leaf cells.

Further reduction in LWP to -0.91 MPa and CS to 0.019 cm s^{-1} probably impaired the PS mechanism since chlorosis occurred indicating greater chlorophyll degradation than synthesis (57). At day 14, when LWP declined to -1.34 MPa and CS to 0.004 cm s^{-1} , there was severe chlorosis and apparent growth cessation. At this stage leaves remained folded probably indicating a cessation in gas exchange processes and complete stomatal closure.

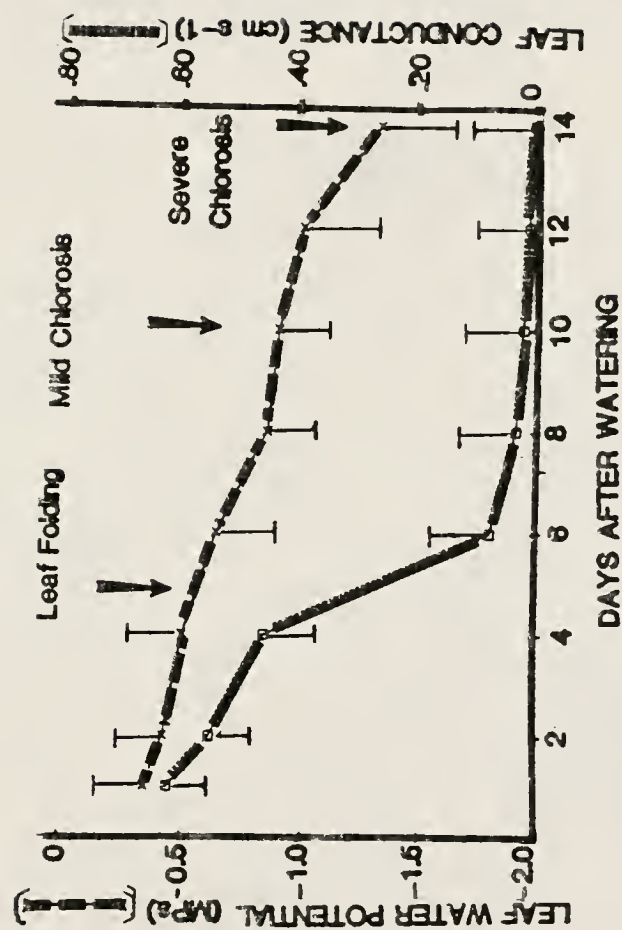


Figure 3-6. Effect of a 14 day drying cycle on leaf water potential and leaf conductance of 'Grande Naine' banana grown under greenhouse conditions. Points are the means of five replicate plants and vertical bars represent the SE.

Experiment 2--ixora. LWP decreased linearly after day 2 but there was a steep decline in CS from 0.53 cm s^{-1} on day 2 to 0.14 cm s^{-1} on day 4 (Figure 3-7). Wilting of youngest leaves occurred between day 4 and 6 and corresponded to decreases in LWP from -1.08 to -1.71 MPa and in CS from 0.14 to 0.038 cm s^{-1} . Severe wilting of top leaves and abscission of bottom leaves were observed on day 8 at a LWP of -2.06 MPa and a CS of 0.008 cm s^{-1} . Plant water status between days 4 and 6 of the cycle was comparable to that at midday (-1.2 MPa) in plants under the W1 irrigation treatment in experiment 1. This indicated that reducing irrigation volume was an effective means of imposing water stress in ixora. Beyond the day 8 stage, wilting and leaf abscission made it difficult to record further data. Since stressed plants were not rewatered it was impossible to determine whether stomatal closure and leaf abscission observed in this study were clearly mechanisms imparting stress tolerance that allowed the plants to survive.

Growth Room

Experiment 3--banana. PS, CS and TR diurnal patterns paralleled one another under the more controlled conditions of the growth room (Figure 3-8) but irrigation treatment effects were not quite as dramatic as in the greenhouse experiment (Figure 3-2). Maximum PS, CS and TR occurred in the growth room at 1000 hr followed by a gradual decline to

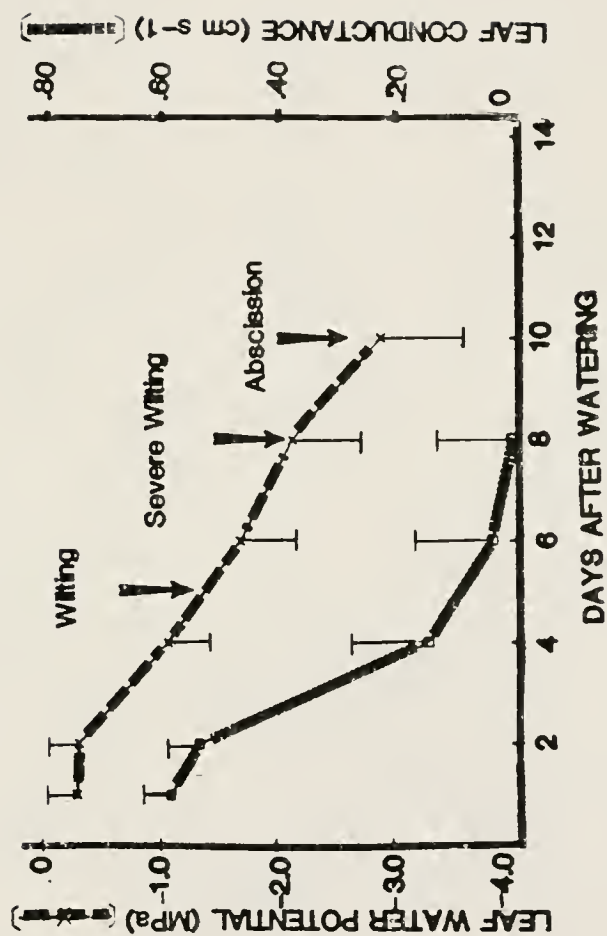
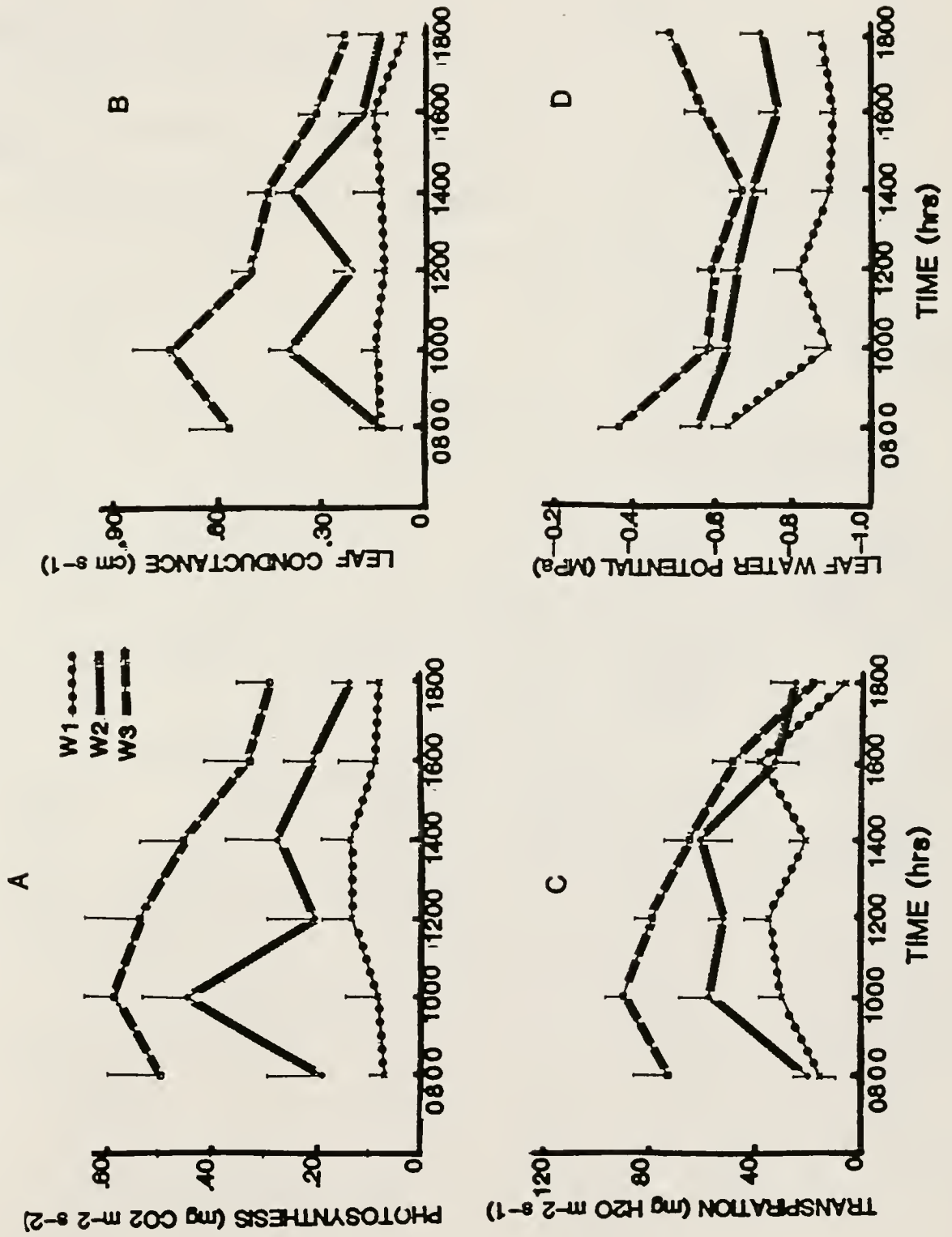


Figure 3-7. Effects of a 14 day drying cycle on leaf water potential and leaf conductance of *Ixora chinensis* L. 'Maui' grown under greenhouse conditions. Points are the means of five replicate plants and vertical bars represent the SE.

Figure 3-8. Effects of three irrigation volumes on the diurnal physiological responses of 'Grande Naine' banana grown under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. W1 = 10 ± 2 ml, W2 = 20 ± 4 ml and W3 = 40 ± 8 ml daily per 150 cm³ container. Points are the means of six replicate plants and vertical bars represent the SE.



1800 hr (Figure 3-8) while maximum levels in the greenhouse experiment were at 1200 to 1400 hr for CS and 1000 to 1400 hr for TR. Higher light intensity early in the day in the growth room could have resulted in earlier stomatal opening (33). Both Shmueli (126) and Chen (25) reported CS and TR diurnal maxima in banana at 1000 hr followed by declines and with minor increases at 1400 hr.

Under the W3 irrigation treatment, maximum PS, CS and TR were $0.596 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, 0.720 cm s^{-1} and $89.2 \text{ mg H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively at 1000 hr. PS, CS and TR were reduced 25%, 48% and 35% at 1000 hr, respectively, by the W2 irrigation treatment compared to the W3 treatment (Figure 3-8A, 3-8B, 3-8C). At the lowest irrigation level, all gas exchange processes remained consistently low throughout the day and maximum PS, CS and TR were $0.097 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, 0.181 cm s^{-1} , and $38.2 \text{ mg H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively.

LWP generally declined for all irrigation treatments after 0800 hr for most of the day with an increase after 1400 hr for the W3 treated plants (Figure 3-8D). Midday LWPs were -0.58 MPa , -0.66 MPa and -0.82 MPa for the W3, W2 and W1 treatments, respectively. LWP between 1000 hr and 1400 hr were not different for the W3 and W2 treatments but LWP was significantly reduced by the W1 irrigation level. Despite the similar LWP between W2 and W3 at 1000 to 1400 hr, significant differences in PS, CS and TR were observed.

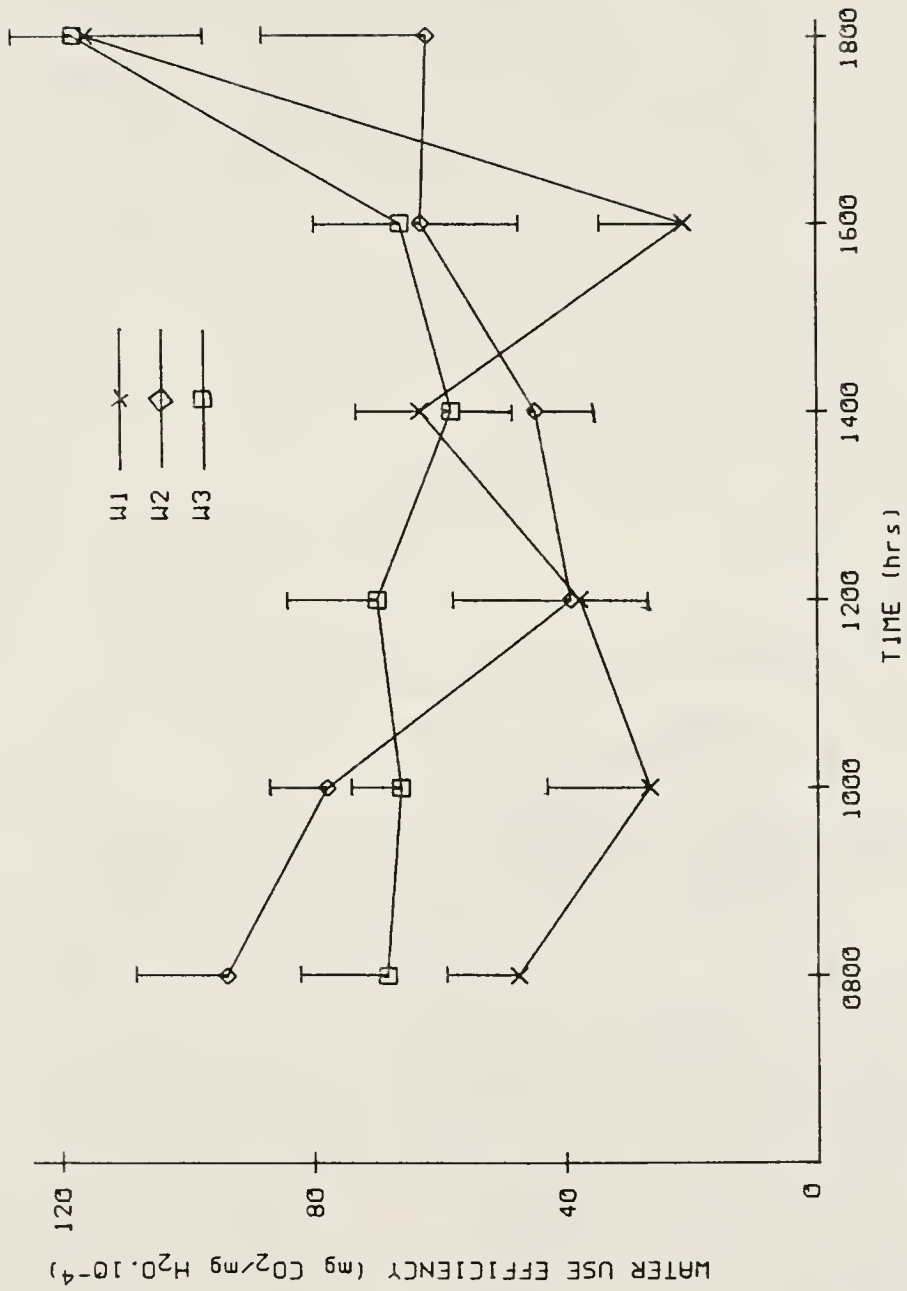
Davies (33) reported increased stomatal sensitivity to decreasing soil water levels for cotton and soybean under

growth chamber conditions but Boyer (14) found PS of sunflower to be affected more by photochemical activity than by stomatal conductance under similar conditions. In the present study there were relative increases in PS but not CS in plants grown in the growth room as compared to the greenhouse.

Maximum CS and TR have been shown to occur in moderately watered field-grown banana at 1000 hr with subsequent declines and smaller peaks at 1400 hr (25,126). It is notable that this response resembled the diurnal patterns that were observed in the W2 treated plants in the present study. In the growth room LWP were generally lower than in the greenhouse and could have been responsible for the general decline in PS, CS and TR after 1000 hr.

Under growth room conditions, the W3 irrigation treatment generally maintained a constant WUE throughout the day (Figure 3-9) reflecting the parallel changes in PS and TR. Though WUE for the W2 treated plants declined at 1200 and 1400 hr compared to 0800 hr, it was still not significantly different from that of the W3 plants during these hours. The relative improvement in WUE at the lowest irrigation in this experiment compared to the same treatment in the greenhouse study was due mainly to increased PS. The W1 irrigation treatment under growth room conditions therefore did not depress physiological responses as much as that observed in the greenhouse study.

Figure 3-9. Effects of three irrigation volumes on the diurnal water use efficiency of 'Grande Naine' banana grown under growth room conditions. $W1 = 10+2$ ml, $W2 = 20+4$ ml and $W3 = 40+8$ ml daily per 150 cm³ container. Points are the means of six \bar{x} replicate plants and vertical bars represent the SE.

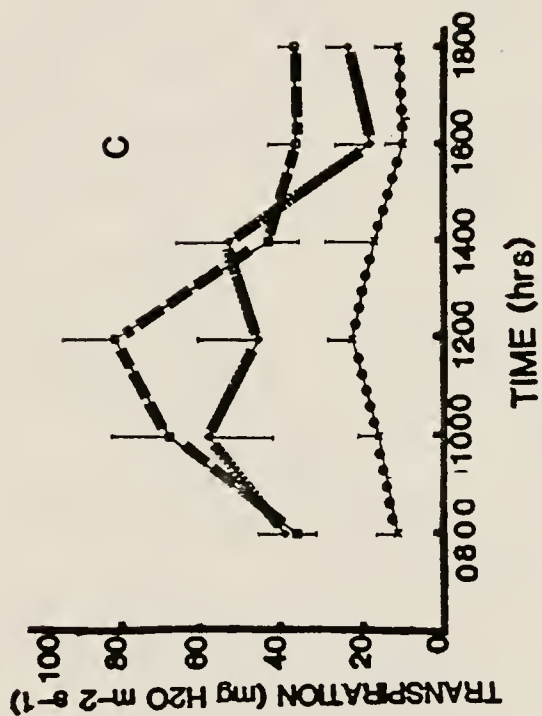
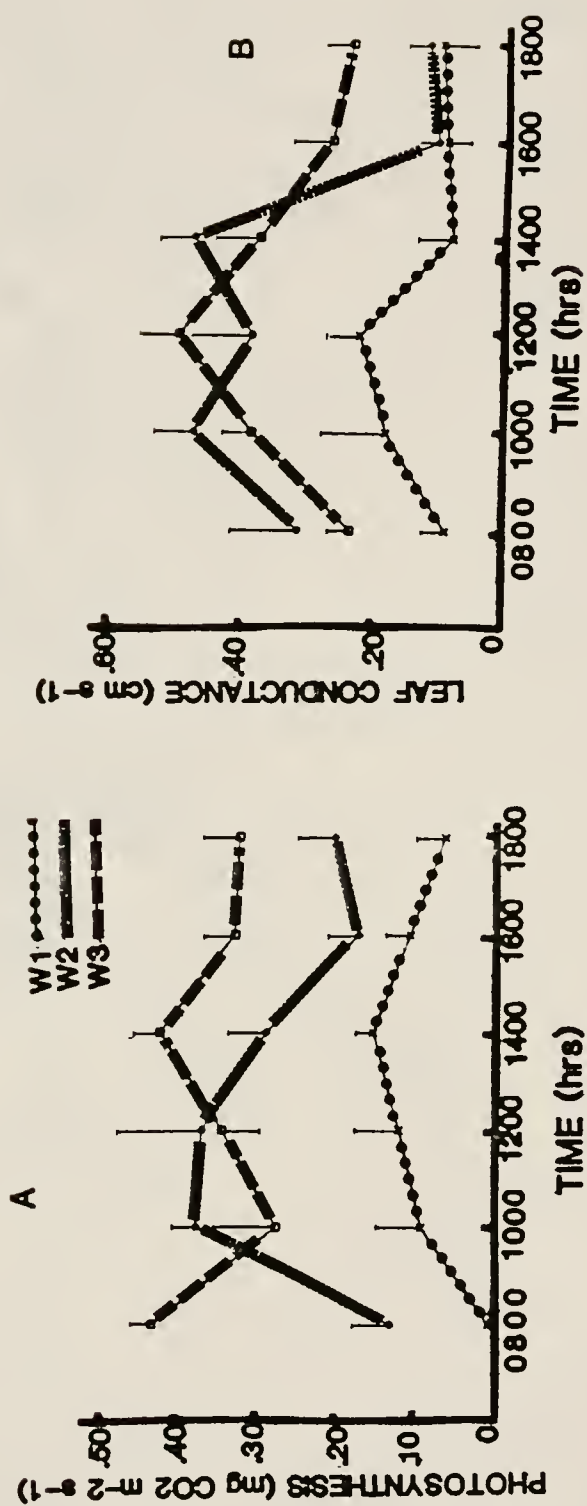


Experiment 3--ixora. Under growth room conditions, the W2 and W1 treatments did not consistently decrease physiological parameters (Figure 3-10) as severely as in the greenhouse study (Figure 3-4). At 1200 hr, there were no differences in responses of plants under the W2 and W3 treatments but at the lowest irrigation treatment, all parameters were significantly reduced over those at the higher irrigation levels.

Maximum PS rates were 0.425, 0.388 and 0.151 mg CO₂ m⁻² s⁻¹ for the W3, W2 and W1 irrigation treatments, respectively (Figure 3-10A). These rates were 1.25, 7 and 10 times higher than the respective rates in the greenhouse study and may have reflected the influence of increased PPFD on PS in ixora, particularly at the lower irrigation treatments. Light levels in the greenhouse were probably below light saturation levels for ixora.

There were no differences in CS between plants at the W2 and W3 irrigation levels from 0800 to 1400 hr but CS was significantly reduced at these hours by the W1 irrigation volume (Figure 3-10B). Midday CSs were 0.492, 0.382 and 0.190 cm s⁻¹ under the W3, W2 and W1 treatments, respectively. Compared with CS in plants in the greenhouse experiment (Figure 3-4B), these values were 34%, 49% and 87% higher at the W3, W2 and W1 irrigation levels, respectively. The increased response in stomatal opening, especially at the lower irrigation levels corresponded with increases in PS.

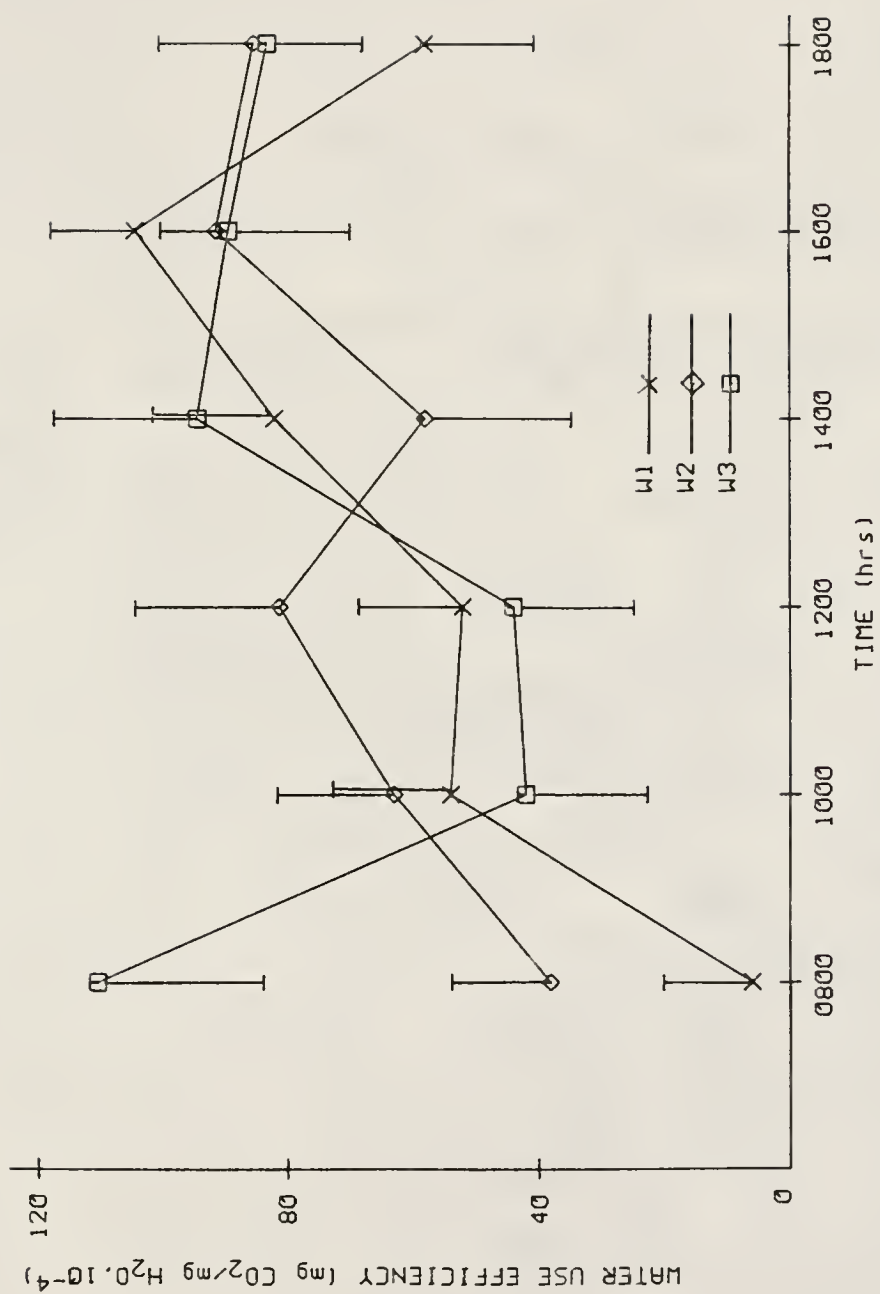
Figure 3-10. Effects of three irrigation volumes on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under growth room conditions. A. leaf photosynthesis B. leaf conductance and C. transpiration. $W1 = 10+2 \text{ ml}$, $W2 = 20+4 \text{ ml}$ and $W3 = 40+8 \text{ ml}$ daily per 150 cm^3 container. Points are the means of six replicate plants and vertical bars represent the SE.



The high PS rate at 0800 hr under the W3 irrigation resulted in a correspondingly high WUE (Figure 3-11) and although WUE then declined at 1000 and 1200 hr for the highest irrigation treatment, WUE values were basically the same for all irrigation treatments through the rest of the day. Under greenhouse conditions, W3 treated plants clearly had higher WUE than plants subjected to lower irrigation levels (Figure 3-5). The increase in WUE in the W2 and W3 relative to the W3 treated plants under growth room conditions was due mainly to the increased PS rates in the high light environment.

Growth room conditions, therefore, not only moderated physiological responses of ixora to reduced irrigation volume but also stabilized PS/TR changes as reflected by WUE values. The increased photosynthetic response in plants grown under the W1 and W2 irrigation volumes suggested that ixora could probably better withstand decreased irrigation volume in the growth room compared to greenhouse conditions reported in this study.

Figure 3-11. Effects of three irrigation volumes on the diurnal water use efficiency of *Ixora chinensis* L. 'Maui' grown under growth room conditions. W1 = 10+2 ml, W2 = $\frac{20+4}{3}$ ml and W3 = 40+8 ml daily per 150 cm³ container. Points are the means of six replicate plants and vertical bars represent the SE.



CHAPTER IV
ROOT-ZONE TEMPERATURE EFFECTS ON BANANA AND IXORA
UNDER TWO GROWING CONDITIONS

Introduction

High root-zone temperatures (RZT) have been shown to reduce plant growth (59,63,70) and affect many physiological processes (43,46,64). Tropical and subtropical plant species are often thought to be heat tolerant, but soil temperatures as high as 52°C have been recorded in the tropics (39), and temperatures in this range can be lethal for some tropical (39,63) and subtropical crops (62). An air temperature of 33°C was reported as being optimum for growth and dry weight partitioning in banana (Musa spp. AAA) (142) and mineral composition was highly influenced by temperatures from 18 to 33°C (143). A RZT of 33°C was found to be optimum for growth and transpiration in coffee (39), a member of the same subfamily of the Rubiaceae to which ixora belongs (6). However, there are no reports on RZT effects on growth and physiology of container-grown banana or ixora.

It is essential to identify growth and physiological effects of high RZT in container production systems before control measures can be developed to alleviate such effects. This study investigated the short-term effects of RZT on

container-grown 'Grande Naine' banana and Ixora chinensis L. 'Maui' under greenhouse and growth room conditions.

Materials and Methods

Plant Materials and General Cultural Procedures

Ten- to 12-cm tissue-cultured 'Grande Naine' banana plants and similar-sized, uniform Ixora chinensis L. 'Maui' rooted cuttings were obtained from commercial nurseries. Plants were hardened in intermittent mist (6 sec min⁻¹) for one week under 80% light exclusion and then moved to 40% light exclusion for another week. Plants were then transplanted to 4-cm diameter x 21-cm high conical containers (150 cm³) using Metro-Mix 300 growth medium (W.R. Grace and Co., Cambridge, MA). Plants were fertilized weekly with a soluble 20N-8.8P-16.6K fertilizer (Peters 20-20-20, W.R. Grace and Co., Cambridge, MA) at 150 ppm N.

Experiment 1--Greenhouse

An experiment was initiated August, 1985 in an air-conditioned glass greenhouse with a mean maximum PPFD of 600 to 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, and a 25^o to 30^oC day and 18^o to 21^oC night temperature. Relative humidity was not controlled and varied from 40% to 80% (Figure 4-1). Recently transplanted banana and ixora plants were watered daily to container capacity and allowed to acclimatize for one week.

RZT treatments were established within styrofoam-lined wooden air bath boxes (1 m x 1 m x 20 cm) in which plant containers were firmly inserted to within 2 cm from their

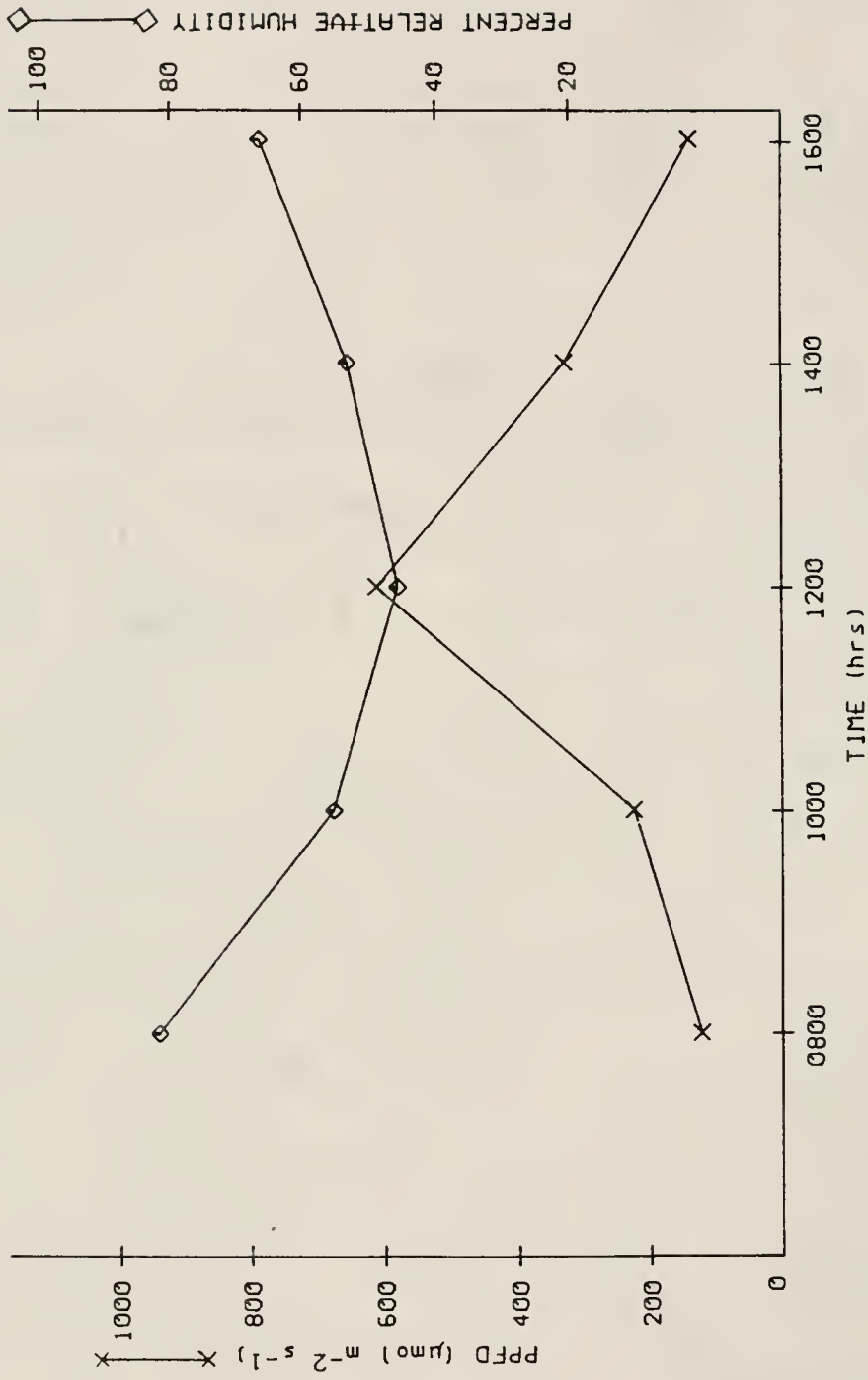


Figure 4-1. Photosynthetic photon flux density and relative humidity in the greenhouse during measurements of physiological parameters.

upper rims. Four equally spaced 100 watt aluminum foil-covered incandescent light bulbs provided convective heating of the enclosed root systems. Proper distribution of heat and aeration within the boxes were ensured by two fans (IMC Magnetics, Roch. NH) per box. The light bulbs in each box were controlled by a pre-set thermostat and the temperatures in each box were verified daily with a thermocouple thermometer (TH 65, Wescor, Inc., Logan, UT). Electrical power to the temperature boxes was controlled by Intermatic Time Controls (Intermatic Inc. Spring Grove, Ill), providing daily RZT treatments from 1000 to 1600 hr. Boxes were placed on 1 m high benches and an automatic drip irrigation system provided daily watering of all plants to container capacity at 2200 hr.

RZT treatments established were $28 \pm 1^{\circ}$, $33 \pm 1^{\circ}$, $38 \pm 1^{\circ}$ and $43 \pm 1^{\circ}\text{C}$. Each temperature box contained six ixora and six banana plants and there were three replicate boxes for each treatment temperature arranged in a randomized complete block design. Species were treated and analyzed as separate experiments. Means and standard errors were calculated for the six replicate plants measured at each sampling time.

After 14 days of RZT treatments, diurnal measurements of leaf photosynthesis (PS), leaf conductance (CS), transpiration (TR) and leaf water potential (LWP) were made using a portable photosynthesis system (LI-6000 model, LICOR, Inc., Lincoln, NE). Measurements were initiated at 0800 hr EDT on a cloudless day and taken every 2 hr until 1600 hr.

A 1-liter cuvette was used and the mean of eight consecutive 30-sec observations constituted a measurement. A zero check of the analyzer was performed between treatments within each replicate. Simultaneous measurements of LWP were made using a pressure chamber (PMS Instrument Model 600, Santa Barbara, CA) as described by Barrett and Nell (9). The third most recently expanded leaf in banana was selected for both gaseous exchange processes and LWP measurements. This leaf has been shown to be the most responsive and the youngest with fully developed stomata (127). The most recently matured ixora leaves were used for PS, CS and TR measurements and 4- to 5-cm shoot tips were sampled for LWP.

Experiment 2--Growth Room

In order to further monitor the physiological responses of ixora and 'Grande Naine' banana to RZT under more precisely controlled environmental conditions, experiment 1 was repeated in a 3.0-m by 7.6-m walk-in growth room. Light irradiance of $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, as measured by a quantum radiometer (LI-COR Model LI-185A, LI-COR Inc., Lincoln, NE), was supplied from 0600 to 1830 hr at plant canopy height by 1000 W phosphor-coated metal-arc HID bulbs (GTE Sylvania Corp., Manchester, NH). Air temperature of 28°C day and 21°C night and a relative humidity of 65% to 70% were maintained.

Each conical container with a transplant was suspended through a tightly fitting styrofoam ring within a specially

constructed root heating tube (RHT). Each RHT was 22.5 cm high and constructed from 7.5 cm diameter metal pipe wrapped with 60 watt 120 vac heating tape (Smith-Gates Corp., Farmington, CT) and 1.25 cm thick foam insulation. The RHTs were connected to solid state electronic controllers which maintained preset treatment temperatures by a thermistor feedback mechanism. Each controller maintained treatment temperatures in 16 tubes with four tubes at each of four specified temperatures. Treatment temperatures were set and also maintained at $28 \pm 0.3^\circ$, $33 \pm 0.3^\circ$, $38 \pm 0.3^\circ$ and $43 \pm 0.3^\circ\text{C}$. Similar leaf number and sampling methods were used and the same physiological measurements were recorded as in experiment 1 after 14 days of root-zone temperature treatments.

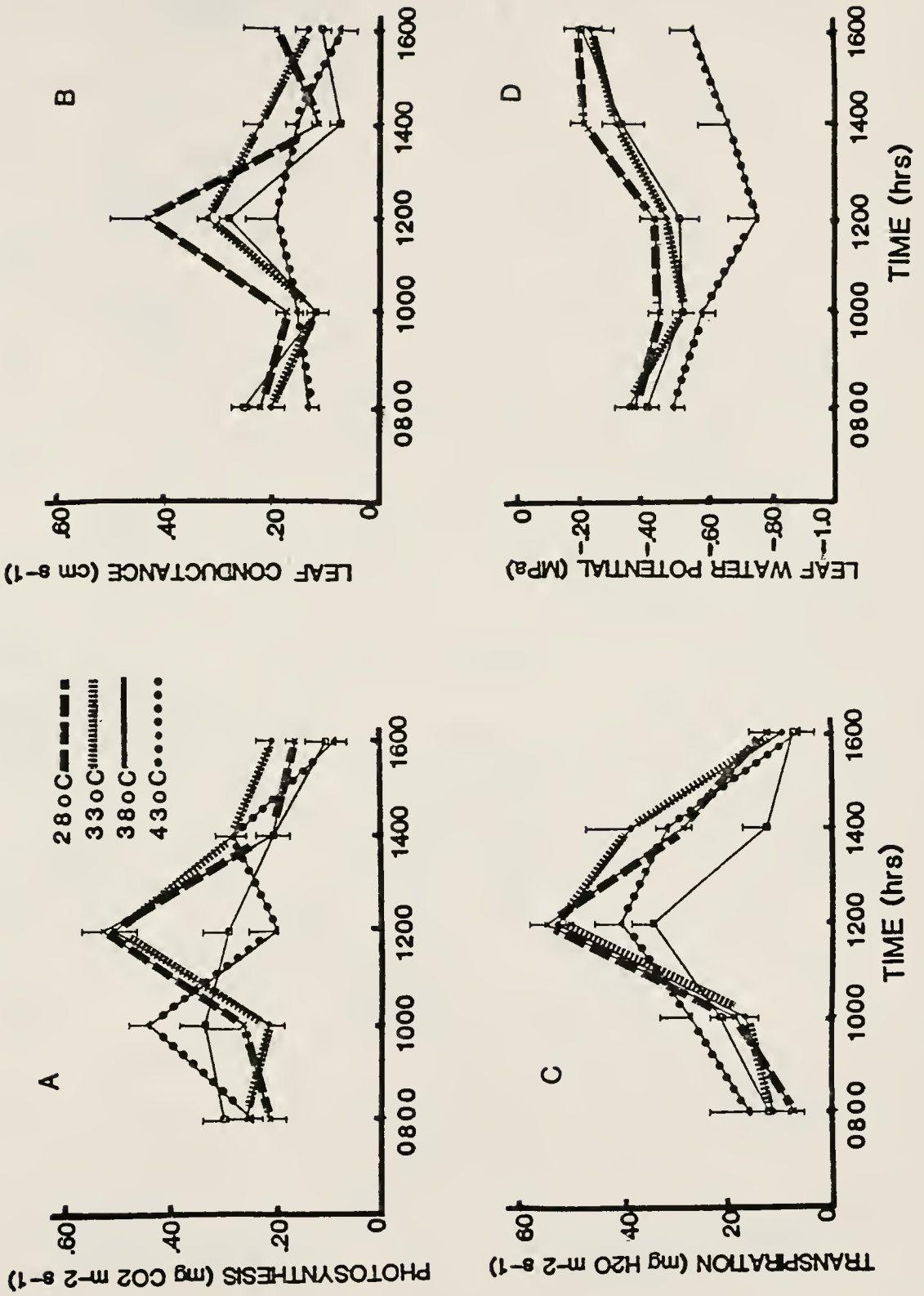
Experimental design was a randomized complete block with 36 plants of each species per temperature treatment arranged in three blocks. Species were treated and analyzed as separate experiments. Means and standard errors were calculated from six replicate plants measured at each sampling time.

Results and Discussion

Experiment 1--Greenhouse

Banana. At the 33° and 28°C RZTs, PS increased to midday maxima of 0.53 and $0.50 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, and then declined (Figure 4-2A). Maximum PS was $0.43 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 1000 hr in the 43°C RZT treated plants, while PS was

Figure 4-2. Effects of four root-zone temperatures on the diurnal physiological responses of 'Grande Naine' banana grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.



0.31 mg CO₂ m⁻² s⁻¹ for plants at the 38°C RZT. These rates were 20% and 42%, respectively, of the maximum PS recorded at 33°C.

Midday CS for the 28° and 33°C RZT treated plants were 0.43 and 0.34 cm s⁻¹, respectively, with significant reductions to 0.28 and 0.19 cm s⁻¹ for plants at the 38° and 43°C RZT (Figure 4-2B). TR diurnal patterns were closely related to those for CS, with maximum rates of 54 and 52 mg H₂O m⁻² s⁻¹ at midday for plants at the 28° and 33°C RZT, respectively (Figure 4-2C). Midday TR was significantly reduced by the 38° and 43°C RZT compared to the other RZTs.

LWPs were generally not different throughout the day for the 28°, 33° and 38°C RZT treated plants. Among these three RZT treatments, a low midday LWP of -0.52 MPa was recorded at the 38°C RZT (Figure 4-2D). A significant reduction in LWP was noted for plants at the 43°C RZT at 1200 hr, with a midday LWP of -0.76 MPa. Although transpirational water loss was reduced in plants at the 43°C RZT at midday compared to plants at the 28° and 33°C RZTs, LWP of plants at the highest RZT were significantly lower than those of the other three RZT treatments. At 38°C, TR was less than at 28° and 33°C RZT but LWPs were the same between these treatments. These responses may suggest impairment of the absorptive and/or conductive capacity of roots in plants exposed to the 43°C RZT.

In summary, PS in banana plants was greatest at the 28° and 33°C RZTs under greenhouse conditions. The 28°, 33° and

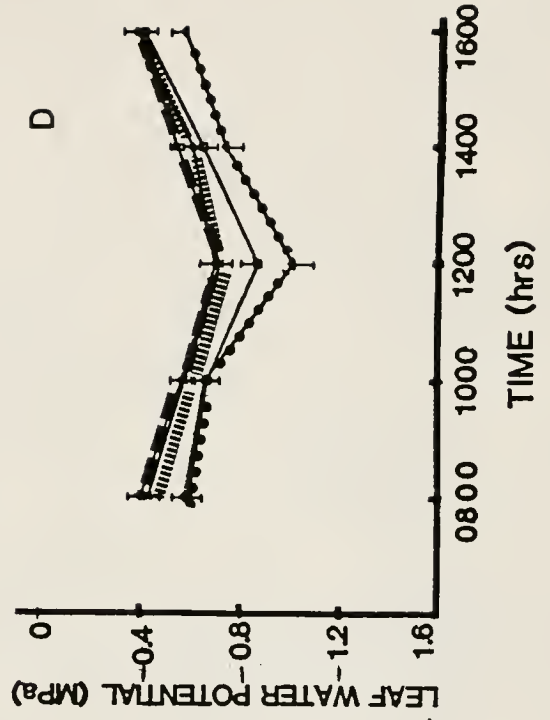
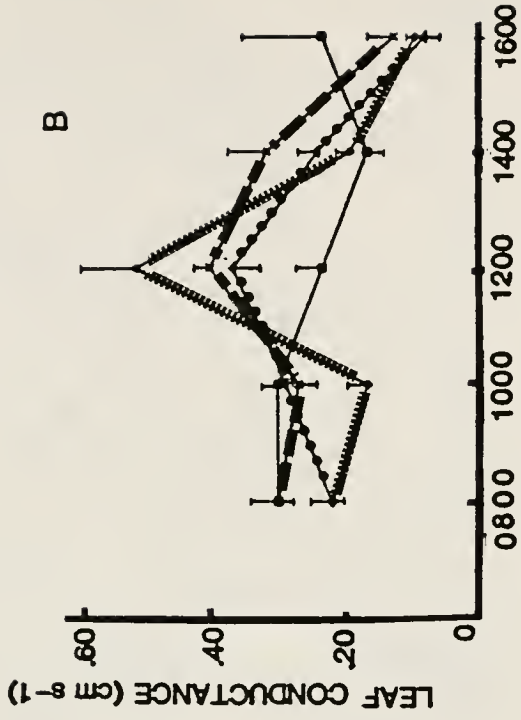
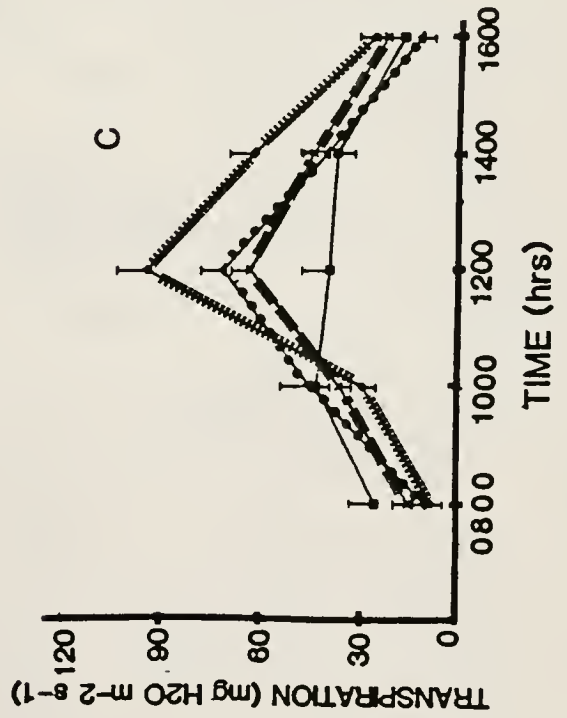
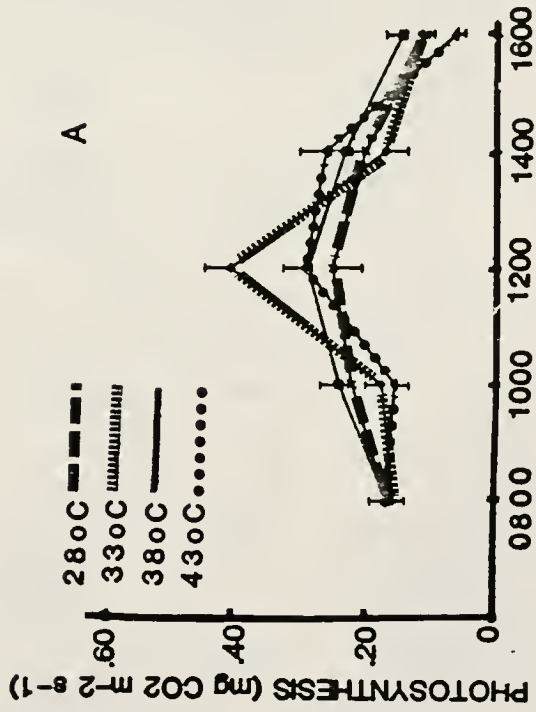
38°C RZT treatments resulted in the highest LWP and the 43°C RZT reduced all measured parameters. RZTs of 28° and 33°C are well within the range of RZTs reported as being optimum for the growth of coffee (39), tomato (42) and pepper (44) while 38°C RZT has reportedly decreased root conductance (146) and transpiration (73).

Ixora. PS in plants at all RZT treatments increased from 0800 hr to midday (Figure 4-3) but PS, CS and TR were greatest at midday in plants exposed to the 33°C RZT. LWP declined for most treatments at 1200 hr, with progressively lower values from the 28° and 33°C RZT to the 38° and 43°C treatments (Figure 4-3D).

Maximum midday PS rate was $0.41 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the 33°C treated plants with reductions to 0.29, 0.28 and $0.25 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the 38°, 43° and 28°C RZT treatments, respectively (Figure 4-3A). At 1400 hr, however, PS rates at the 43° and 38°C RZT were 0.26 and $0.23 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, while PS at 33°C RZT had declined to $0.17 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. At 1600 hr, PS rates for the 28°, 33° and 38°C RZT treated plants were not different. The 33°C RZT clearly resulted in the highest midday PS but because this RZT did not alter morning rates and caused rapid post-midday declines, mean daily PS at 33°C was probably similar to that at other RZT treatments.

CS and TR diurnal patterns were closely related, with the midday maxima of 0.53 cm s^{-1} and $95 \text{ mg H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively, for both parameters occurring in the 33°C RZT

Figure 4-3. Effects of four root-zone temperatures on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.



plants (Figure 4-3B, 4-3C). Midday CS and TR were significantly reduced in plants at the 43°C RZT compared to the 33°C RZT but the 38°C RZT resulted in the lowest midday TR and CS.

Mean midday LWP for plants at the 28° and 33°C RZT was -0.71 MPa with progressive reductions by the 38°C (-0.87 MPa) and 43°C (-1.02 MPa) RZT treatments (Figure 4-3D).

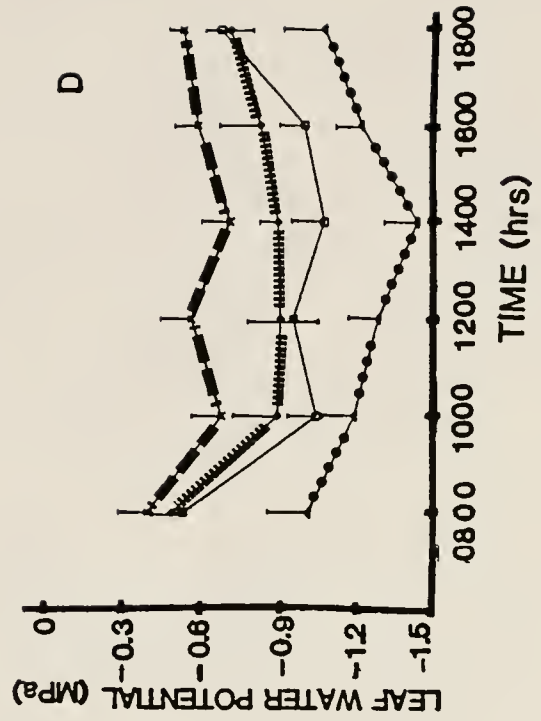
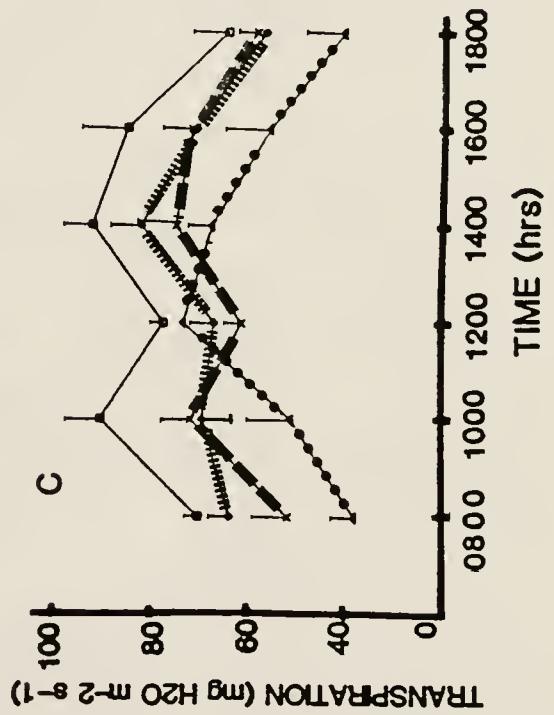
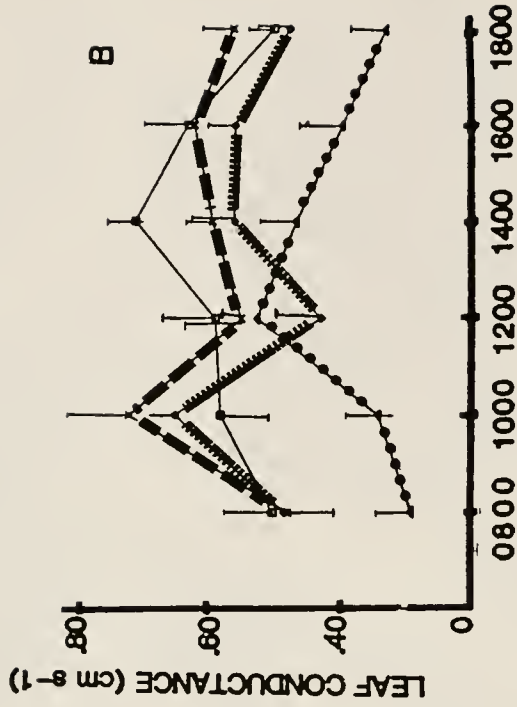
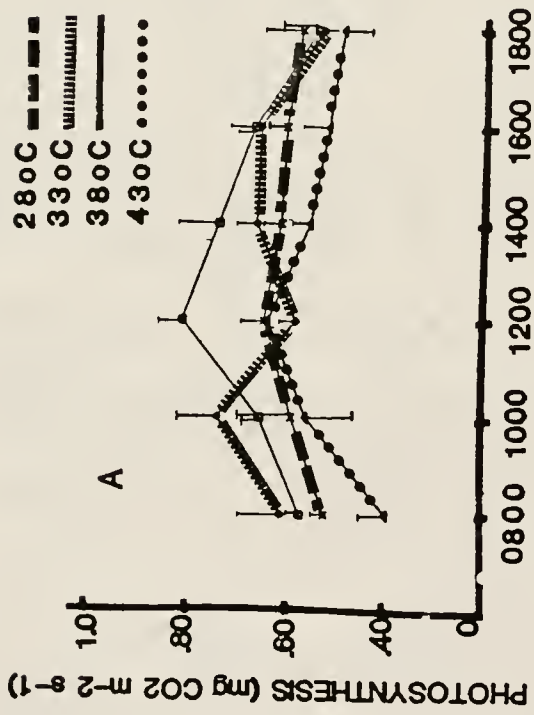
The 33°C RZT treated ixora plants exhibited highest midday PS, CS, TR and had relatively good plant water status compared with other RZT. Although PS was not measured, Franco (39) reported that a RZT of 33°C was optimum for coffee in terms of TR and root and shoot dry weights. TR and plant dry weights were reduced with increasing RZT above 33°C and plants died at 48°C RZT.

Midday LWPs decreased significantly to -0.87 MPa by the 38°C RZT treatment and to -1.02 MPa by the 43°C RZT treatment, but visible symptoms of water stress were never apparent in these plants. In contrast, water-stressed ixora plants (experiment 2, chapter III) exhibited wilting around a LWP of -1.08 MPa. Therefore, there may have been mechanisms to maintain turgor under decreasing LWP in plants at the 38° and 43°C RZT or plants may have become conditioned to the high RZTs.

Experiment 2--Growth Room

Banana. Plants held at the 38°C RZT under growth room conditions (Figure 4-4A) had a maximum midday PS rate of 0.81 mg CO₂ m⁻² s⁻¹, which was a 54% increase over the

Figure 4-4. Effects of four root-zone temperatures on the diurnal physiological responses of 'Grande Naine' banana grown under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.



corresponding greenhouse rate (Figure 4-2A). The 33°C RZT induced a rate of $0.74 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 1000 hr while the 43°C RZT treated plants had the lowest PS rate of $0.39 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 0800 hr and through the afternoon hours (Figure 4-4A).

Maximum stomatal opening for the 28° and 33°C RZT occurred earlier in the day than for the higher RZT treatments (Figure 4-4B). While maximum CS of 0.72 and 0.63 cm s^{-1} occurred in plants at 1000 hr under the 28° and 33°C RZT respectively, peak values for the 43° and 38°C RZT were 0.52 at midday and 0.70 cm s^{-1} at 1400 hr, respectively (Figure 4-4B). The 43°C RZT caused significant reductions in CS and TR from 0800 hr to 1000 hr and later in the day at 1800 hr. Highest TR rates occurred with the 38°C RZT with values of 94.2 and 92.7 $\text{mg H}_2\text{O m}^{-2} \text{ s}^{-1}$ at 1000 and 1400 hr, respectively (Figure 4-4C).

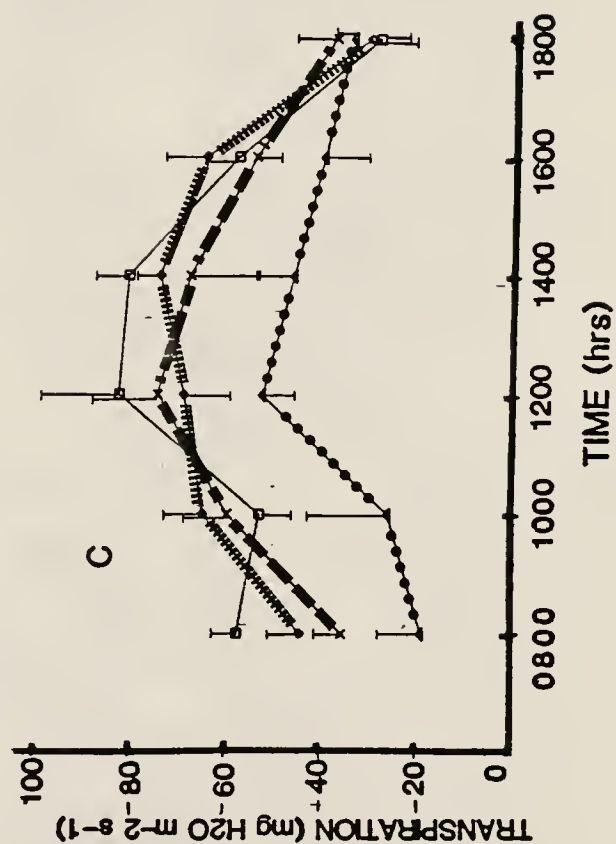
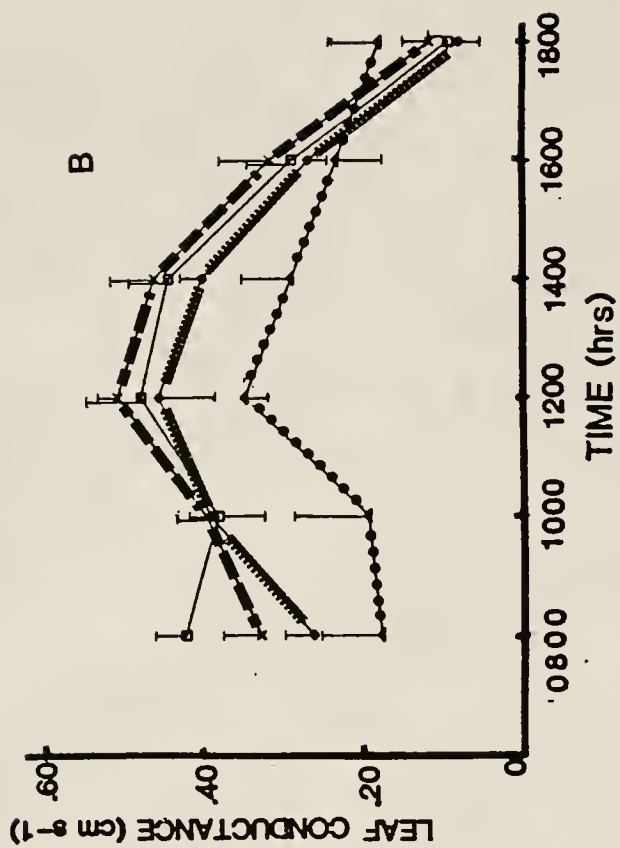
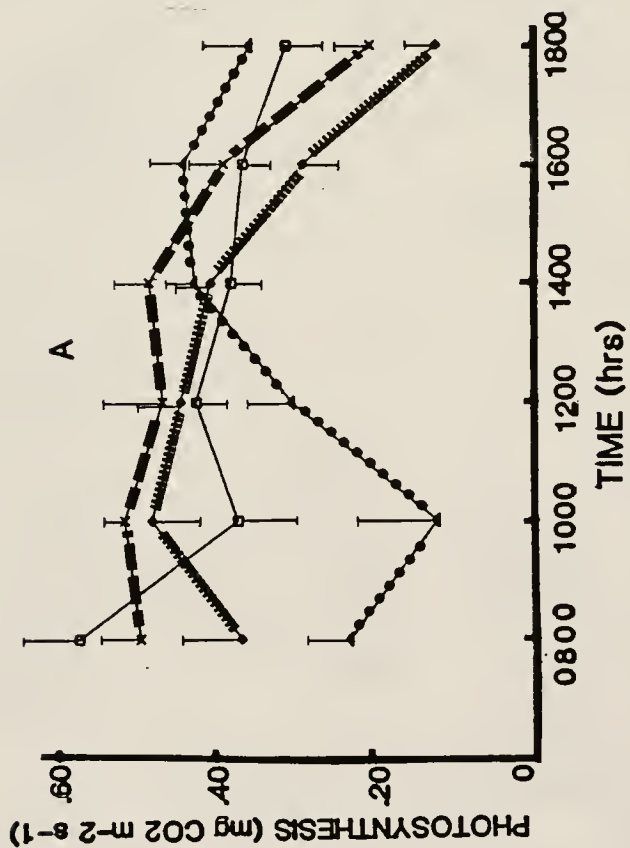
Diurnal patterns of LWP were significantly influenced by RZT treatments (Figure 4-4D). The 28°C RZT treated plants had the highest midday LWP of -0.55 MPa, which was higher than the LWP at the 33° and 38°C RZT treatments. The lowest midday LWP of -1.26 MPa was induced by the 43°C RZT. Overall, LWP were lower in plants in this experiment than those observed in the greenhouse environment. This could be attributed to the higher CS and TR rates that were exhibited by plants in the growth room experiment compared to the greenhouse. In both environmental conditions, however, the highest RZT of 43°C induced the lowest LWP with higher LWP at lower RZTs.

Although the 38° and 43°C RZTs appeared to induce water stress in banana as reflected by low LWP, there was no leaf folding and/or chlorosis as shown by plants that had been water stressed to -0.52 and -0.66 MPa by irrigation treatments under greenhouse and growth room conditions, respectively (experiments 1,3 Chapter III).

Under growth room conditions, the 33° and 38°C RZTs induced the highest PS rates though at different times of the day. Under sunlit growth room conditions, 33°C air temperature was reported as being optimum for growth and partitioning in Cavendish banana but 37°C caused leaf injury (142). Since growth measurements were not recorded in this study it was impossible to determine whether the increased PS observed at 38°C RZT resulted in increased growth or was merely a response to the increased root sink demand for photosynthates. The response of the banana plants grown at 38°C RZT in the two environmental conditions would indicate a greater tolerance to RZTs up to 38°C under growth room conditions. The 43°C treatment was supraoptimal under both environments.

Ixora. Maximum PS, CS and TR at midday followed by distinct declines were not as evident in ixora plants under growth room conditions (Figure 4-5) as they were in the greenhouse study (Figure 4-3). In plants subjected to the 28° and 33°C RZT treatments, PS rates of 0.51 and 0.47 mg CO₂ m⁻² s⁻¹, respectively, were recorded at 1000 hr and followed by a gradual decline to 0.21 and 0.12 mg CO₂ m⁻² s⁻¹,

Figure 4-5. Effects of four root-zone temperatures on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under growth room conditions. A. leaf photosynthesis B. leaf conductance and C. transpiration. Points are the means of six replicate plants and vertical bars represent the SE.



28°C —○—
 33°C - - -
 38°C —△—
 43°C◇.....

respectively, at 1800 hr (Figure 4-5A). A PS rate of $0.57 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was observed at 0800 hr in the 38°C RZT treated plants and was followed by a significant decline at 1000 hr with no further decreases for the rest of the day. PS rates were reduced during the morning hours in plants treated with the 43°C RZT relative to other treatments but increased to levels comparable to other RZTs at 1400 and 1600 hr. Except for shifts in time at which maximum daily PS occurred, there appeared to be little differences in overall PS values between RZT treatments.

Diurnal CS (Figure 4-5B) and TR (Figure 4-5C) followed the same general pattern. Maximum values for both parameters occurred at 1200 and/or 1400 hr in plants treated with either the 28° , 33° or 38°C RZT, with subsequent declines for the rest of the day. Maximum CS recorded for these RZTs was 0.51 cm s^{-1} at 1200 hr which was comparable to the corresponding midday CS in the greenhouse. However, a CS of 0.46 cm s^{-1} at 1400 hr in the growth room experiment represented a 30% increase over the CS recorded at this hour in the greenhouse. A similar pattern was observed for TR. Maximum TR was 83.3 and 80.1 $\text{mg H}_2\text{O m}^{-2} \text{ s}^{-1}$ at 1200 and 1400 hr, respectively. CS and TR were significantly reduced throughout most of the day in the 43°C RZT treated plants (Figure 4-5B, 4-5C).

Under growth room conditions, therefore, RZTs of 28° , 33° and 38°C did not produce appreciable differences in physiological responses in ixora. The relatively low PS, CS

and TR early in the day with subsequent increases at later hours in the 43°C treated plants suggested a lag effect of this RZT on stomatal opening.

Midday CS and TR were comparable to those observed in the greenhouse. However, higher values for these parameters were recorded at 1400 hr and later in the growth room as compared to the distinct post-midday declines in the greenhouse. There was an apparent effect of the constant high light intensity during the illumination period in the growth room that maintained midday stomatal opening to later hours. However, the eventual decline in gas exchange processes at 1800 hr in the growth room suggested that the stomata may not have completely lost the diurnal rhythmic pattern evident under greenhouse conditions.

CHAPTER V
ROOT-ZONE TEMPERATURE AND SOIL MOISTURE EFFECTS ON
BANANA AND IXORA UNDER TWO GROWING CONDITIONS

Introduction

High temperature and water stress often occur simultaneously in crop situations and alleviating the latter is often considered a remedy for the former. Although many drought tolerant plants are also heat tolerant (85), interactions and sometimes negative correlations occur between heat and drought stress (102). Research has tended to concentrate on water and temperature stress effects separately with little emphasis on defining or separating the characteristics of these two stress factors.

Suboptimal root-zone temperature (RZT) (7,8,18) and temperate plant species (5,18,69) have been employed in most of the reported investigations that involve RZT and soil moisture interactions. Barlow (7) found that increased shoot carbohydrate under reduced soil moisture was offset by increasing RZT in corn seedlings. Kaufmann (69) found that soil water deficits directly affected leaf water potential (LWP) and transpiration (TR) in 'Monterey' pine seedlings but RZT had no consistent effects on TR and CS. Water stress has

been shown to affect growth (31,116), yield, WUE (10,11,40) and physiological responses (25,126) in banana (Musa spp. AAA). Relatively fewer studies have been reported on temperature stress effects (63,142,143). An air temperature of 33°C was reported as being optimum for growth and dry weight partitioning in Cavendish banana (142) but the investigators experienced some difficulty in separating the stress effects of air temperature and induced vapor pressure deficits. Investigations in banana involving both stress factors simultaneously have not been reported. A similar pattern of research exists for coffee, a major tropical crop that belongs to the same subfamily as ixora (Ixora chinensis L. 'Maui') (6).

This study investigated the effects of four RZTs and two irrigation volumes on growth, physiology and carbohydrate status of 'Grande Naine' banana and 'Maui' ixora under greenhouse and growth room conditions.

Materials and Methods

Plant Materials and General Cultural Procedures

Ten- to 12-cm tissue-cultured 'Grande Naine' banana plants and 12 to 15 cm uniform ixora rooted cuttings were obtained from commercial nurseries. Plants were hardened in intermittent mist (6 secs min⁻¹) under 80% light exclusion for one week and then moved to 40% light exclusion for another week. Plants were transplanted to 6.5-cm diameter x 25.0-cm tall conical containers (555 cm³) using Metro-Mix 300

growth medium (W.R. Grace and Co., Cambridge, MA). Plants were then moved to the experimental greenhouse or growth room where they were watered to container capacity daily and allowed to acclimatize for one week prior to the initiation of the experiment.

Experiment 1--Greenhouse

Experiment 1 was initiated in August, 1985, in an air-conditioned greenhouse in which maximum irradiance levels ranged from 600 to 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, and 25° to 30°C day and 18° to 21°C night temperatures were maintained. Relative humidity was not controlled and varied from 40% to 80% (Figure 5-1).

Two irrigation volumes and four RZT treatments were factorially combined in a split plot design experiment. Plants were watered daily at 2200 hr with 50 \pm 5 ml (W1) and 100 \pm 10 ml (W2) per container (555 cm³). These volumes represented 60% to 70% and 85% to 100% container capacity (CC), respectively. Water was applied automatically through drip tubes by a battery-operated controller (Water Watch Corp. Seattle, WA). The W1 and W2 irrigation treatments were applied by one and two 6-cm dramm irrigation rings/container, respectively.

RZTs of 28 \pm 1°, 33 \pm 1°, 38 \pm 1° and 43 \pm 1°C were established in air-bath boxes as described in Chapter IV. Each temperature box contained six ixora and six banana plants to which the irrigation treatments W1 and W2 were randomly

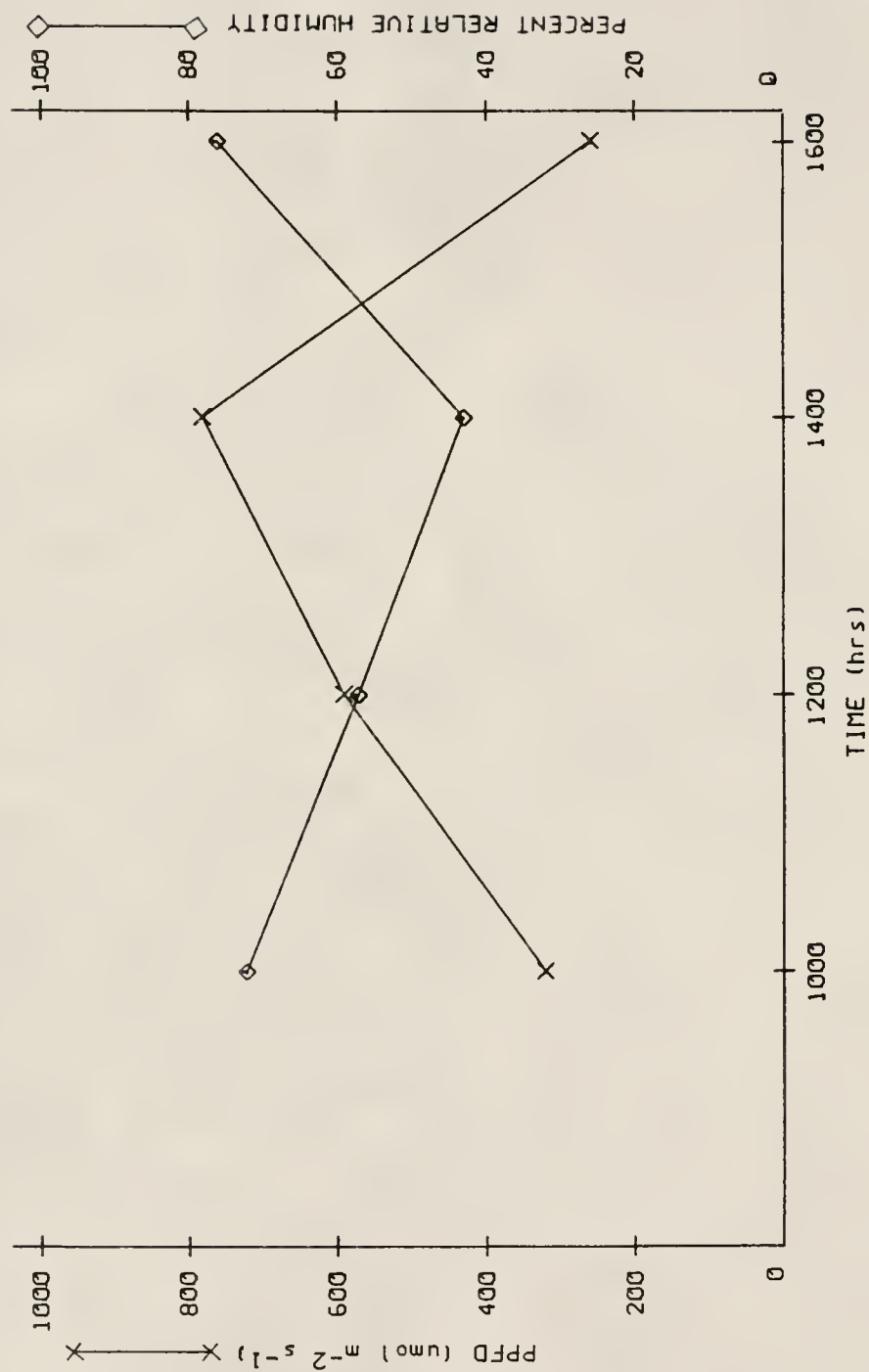


Figure 5-1. Photosynthetic photon flux density and relative humidity in the greenhouse during measurements of physiological parameters.

assigned to three plants per species per treatment. Temperature boxes were replicated three times. RZT treatments were applied daily from 1000 to 1600 hr EDT and irrigation was supplied at 2200 hr so that the imposition of temperature and irrigation treatments did not overlap. Plants were fertilized weekly with the appropriate volume of water and concentrations of 20N-8.8K-16.6P fertilizer (Peters 20-20-20, W.R. Grace and Co., Cambridge, MA) to apply 250 mg N/container. Fertilizer was applied with a hand operated injector (Chem-trol Inc, Kansas City, KS).

Plant height, leaf area, leaf number and stem diameter for banana, and plant height, plant width, shoot number and total axillary shoot length for ixora were recorded weekly. Plant height was considered the distance from the soil surface to the leaf apex in banana and to the stem tip in ixora. Banana stem diameter was measured at pot rim level and leaf area of the third newest leaf was calculated from 0.65 of leaf length multiplied by leaf width (127). Leaf numbers were derived from the number of whole green functional leaves and emerging leaves were assigned a value of 0.25, 0.50 or 0.75 depending on the fraction of the leaf lamina fully exposed.

Ten weeks after the initiation of the experiment, leaf photosynthesis (PS), leaf conductance (CS) and transpiration (TR) were recorded on a cloudless day from 1000 to 1600 hr at 2-hr intervals using a portable photosynthesis system (Model LI-6000, LI-COR Inc., Lincoln, NE). A 1-liter leaf cuvette

was used and the mean of eight 30-sec observations constituted a measurement. A zero check of the analyzer was performed between treatments within each replicate. Simultaneous measurements of LWP were made using a pressure chamber (PMS Instrument Model 600 Santa Barbara, CA) as described by Barrett and Nell (9). The third most recently expanded leaf in banana was selected for gas exchange processes and LWP measurements. This leaf has been shown to be the most responsive and the youngest with fully developed stomata (127). The most recently-matured ixora leaves were used for PS, CS and TR measurements but 4- to 5- cm shoot tips were sampled for LWP.

After physiological measurements, leaf and root samples were immediately collected for carbohydrate analysis. The third newest leaf in banana and six of the most fully developed leaves in ixora were sampled. A 5- to 7-g composite sample of carefully washed roots was used for root carbohydrate analysis. Plants were then separated into leaves, stems and roots before drying for at least 48 hr in a forced-air oven at 70°C prior to recording dry weights.

Ethanol-soluble sugars and starch were determined according to the procedure used by Stamps (133) in which free sugars were extracted from a 50-mg sample with 80% ethanol. Leaf and root tissues were first freeze-dried at -40°C (Freezemobile II, Virtis Co. Gardner, NY) for at least 72 hr and stored in a desiccator. Tissue was then ground through a 20-mesh screen (Wiley Mill, Philadelphia, PA) and a 50-mg

sample was boiled in 8 ml of 80% ethanol and centrifuged for 1 hr at 10,500 rpm (Model HT Centrifuge, International Equipment Co., Division of Damon). A 0.5-ml sample of supernatant was diluted from 10 to 20 times with deionized water. One half milliliter of 5% phenol and 2.5 ml concentrated H_2SO_4 were added to 0.5 ml of each diluted sample and the mixture was allowed to cool. Absorbance was then measured at 490 nm using a spectrophotometer. Free sugar concentrations were determined from plots of absorbance by standard solutions of D-glucose and deionized water. Starch content was determined by incubating the centrifuged pellet at 34°C for 12 hr in 5 ml of an enzyme solution containing sodium phosphate mono- and dibasic, alpha-amylase, amyloglucosidase and anhydrous calcium chloride. After incubation, samples were centrifuged for 1 hr and absorbance determined using the same procedure as above.

The experiment was arranged in a split plot design with three blocks in which RZT were main plots and irrigation treatments represented subplots. Each species was treated and analyzed as a separate experiment. Mean values of physiological measurements were plotted across time to reveal diurnal patterns and regression analyses of midday physiological parameters over RZT were performed for each irrigation volume treatment. Weekly leaf area data of banana were used for growth over time plots and final growth and carbohydrate measurements were used for regression analyses over RZT and irrigation treatments. Single degree-of-freedom

orthogonal comparisons between treatment means were performed and partitioning of interactions for linear, quadratic and cubic models for final growth and carbohydrate data were made using the General Linear Model procedure of the Statistical Analysis System (134).

Experiment 2--Growth Room

In order to further monitor the physiological responses of banana and ixora to RZT and irrigation treatments under more precisely controlled environmental conditions, experiment 1 was repeated in a walk-in growth room in August and September, 1986. The growth room was described in Chapters III and IV. Irrigation and RZT treatments were the same as for experiment 1 but root heat tube (RHT) containers as described in Chapter III were used. Similar plant materials and cultural procedures were used as for experiment 1 except plants were first transplanted for one week into 4-mil 7.5 cm diameter x 22.5 cm tall clear plastic bags (1200 cm³) that were inserted into similar sized lengths of PVC tubes. One week prior to the initiation of treatments, the plastic bags were transferred to RHTs in the growth room. Irrigation volumes of 75 \pm 8 ml (W1) and 150 \pm 15 ml (W2) per container were applied daily at 2200 hr as in experiment 1. These volumes provided 60% to 70% container capacity (CC) and 85% to 100% CC, respectively. Water was applied automatically by drip irrigation and one and two 1-mm drip tubes per container constituted the W1 and W2 treatments, respectively.

There were 16 RHTs per electronic controller, four of which were randomly assigned to each RZT of $28 \pm 0.3^\circ$, $33 \pm 0.3^\circ$, $38 \pm 0.3^\circ$ and $43 \pm 0.3^\circ\text{C}$. There were six replicate plants per RZT-irrigation treatment arranged in a randomized complete block design with three blocks. Species were organized and treated as separate experiments. RZT treatments were applied from 1000 hr to 1600 hr daily.

Six weeks later PS, CS, TR and LWP were measured at 2 hr intervals from 0800 to 1800 hr and growth data and samples for carbohydrate analysis were taken as described in the greenhouse experiment. Chlorophyll concentration of leaves used for physiological measurements was recorded using a Spad 501 chlorophyll light absorbance meter (Minolta Corp. Ramsey, NJ) and expressed as $\mu\text{mol m}^{-2}$.

Means and standard errors were calculated from physiological measurements of six replicate plants at each sampling time and are shown with data points. Single degree-of-freedom orthogonal comparisons between treatment means and partitioning of interactions for linear, quadratic and cubic models for growth, physiological and carbohydrate data were made using the General Linear Model procedure of the Statistical Analysis System (134).

Results and Discussion

Experiment 1--Greenhouse

Physiological responses--banana. Under the W1 irrigation volume, maximum PS at 1200 and 1400 hrs was 0.285 and 0.263 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively (Figure 5-2A). Diurnal patterns for CS and TR appeared to parallel each other under both irrigation levels with maximum levels for both parameters occurring at 1200 and 1400 hr (Figure 5-2, 5-3). LWPs were generally higher in plants at the 28° and 33°C RZTs under the W1 irrigation volume except at midday when LWP averaged -0.71 MPa over all RZTs (Figure 5-2D).

At the higher irrigation level, W2, a maximum PS of 0.330 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ was measured for the 33°C RZT treated plants at midday (Figure 5-3A) and another similar peak of 0.301 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ occurred in the 38°C RZT treated plants at 1400 hr. PS was significantly reduced at midday and thereafter by the 43°C RZT. LWPs were generally higher in the 33° and 38°C RZT treated plants compared to those observed at 28° and 43°C between 1000 and 1400 hr (Figure 5-3D).

Regression analyses of midday PS over RZT and irrigation treatments revealed significant effects of RZT but not irrigation treatments (Figure 5-4A). PS was highest at the 28° and 33°C RZT treatments with progressive reductions at the 38° and 43°C RZTs. While highest midday PS was noted for the 28° and 33°C RZTs, diurnal patterns showed a lag in response for the 38°C RZT with peak PS occurring after midday (Figure 5-2A, 5-3A). Since there were also corresponding

Figure 5-2. Effects of four root-zone temperatures and a 50+5 ml daily irrigation volume per 555 cm³ container on the diurnal physiological responses of 'Grande Naine' banana grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

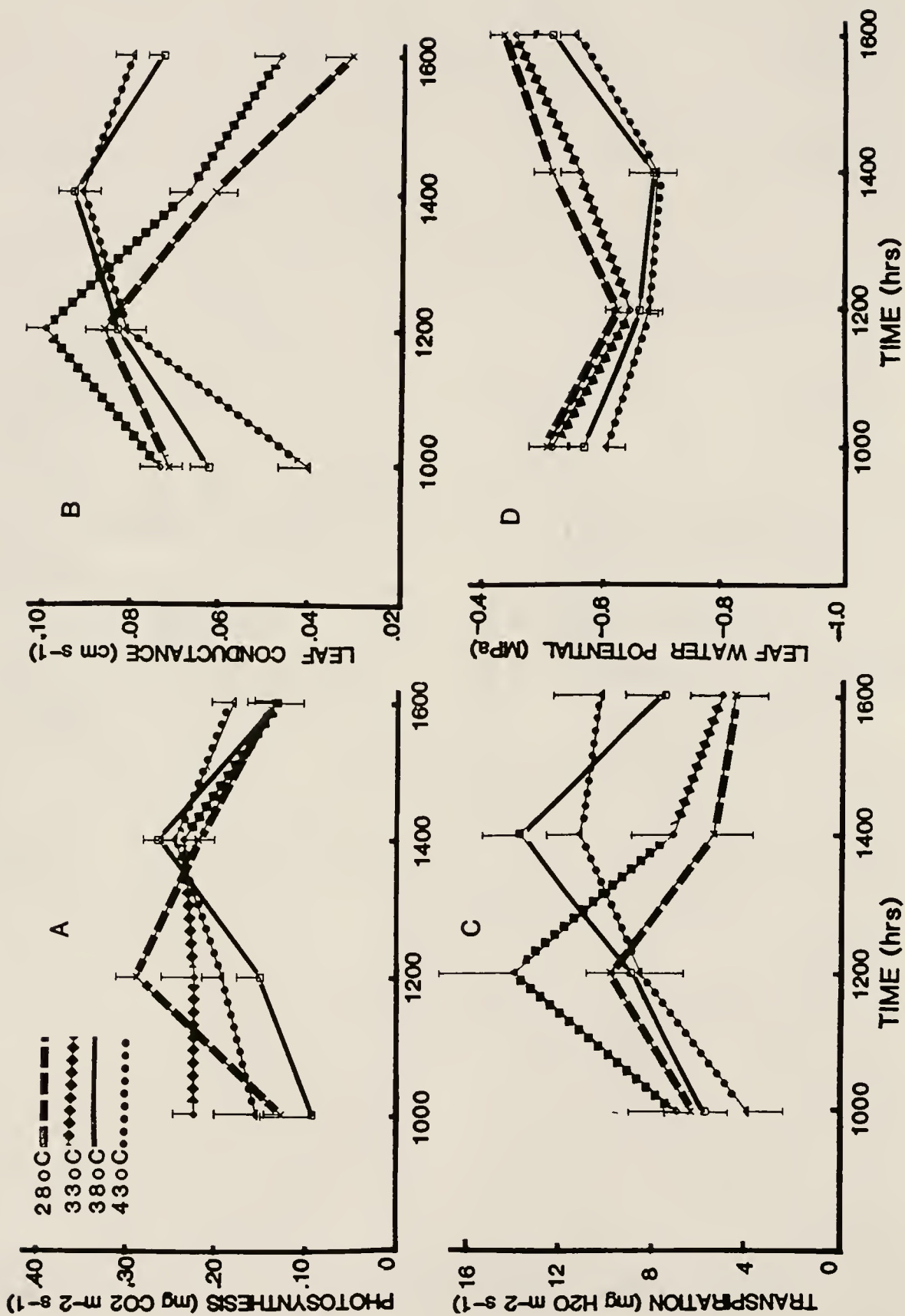


Figure 5-3. Effects of four root-zone temperatures and a 100+10 ml daily irrigation volume per 555 cm³ container on the diurnal physiological responses of 'Grande Naine' banana grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

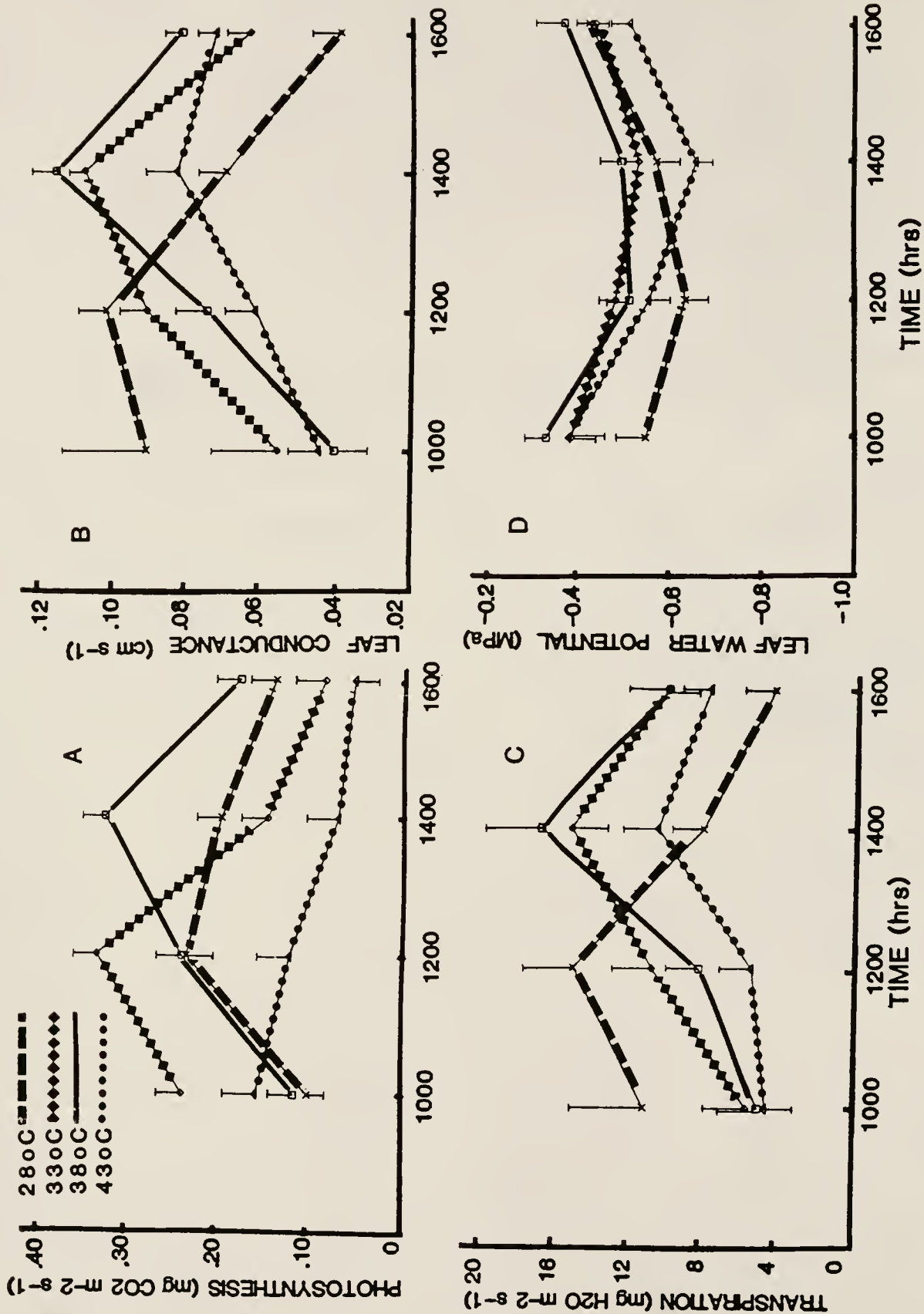
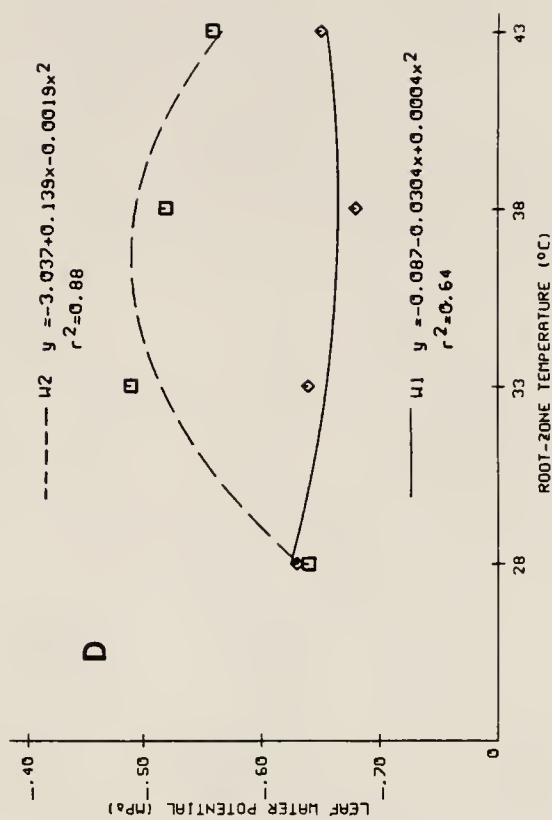
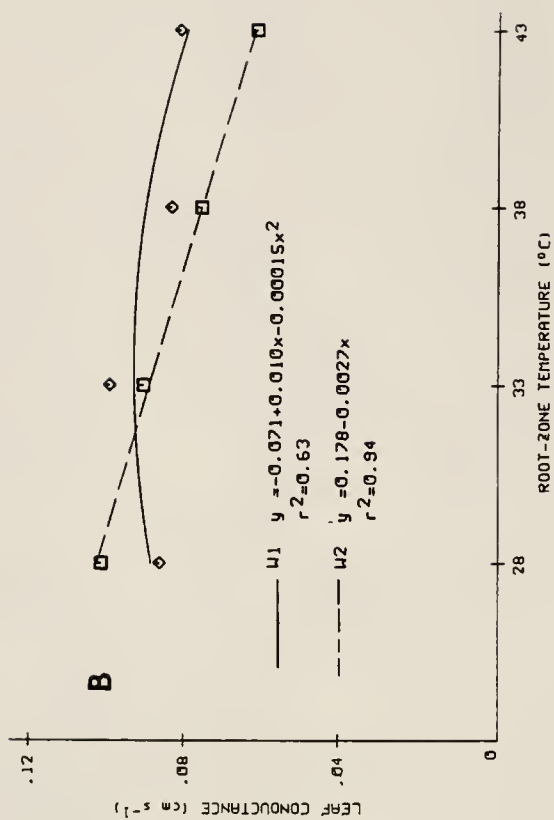
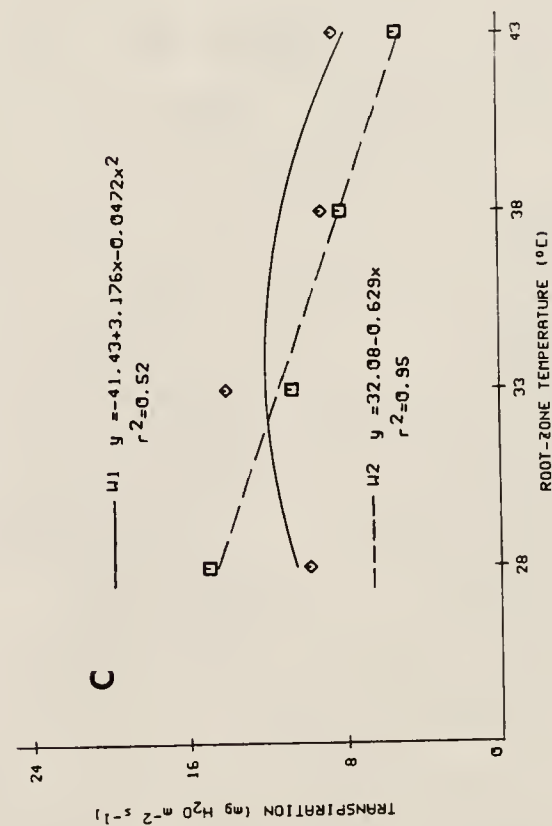
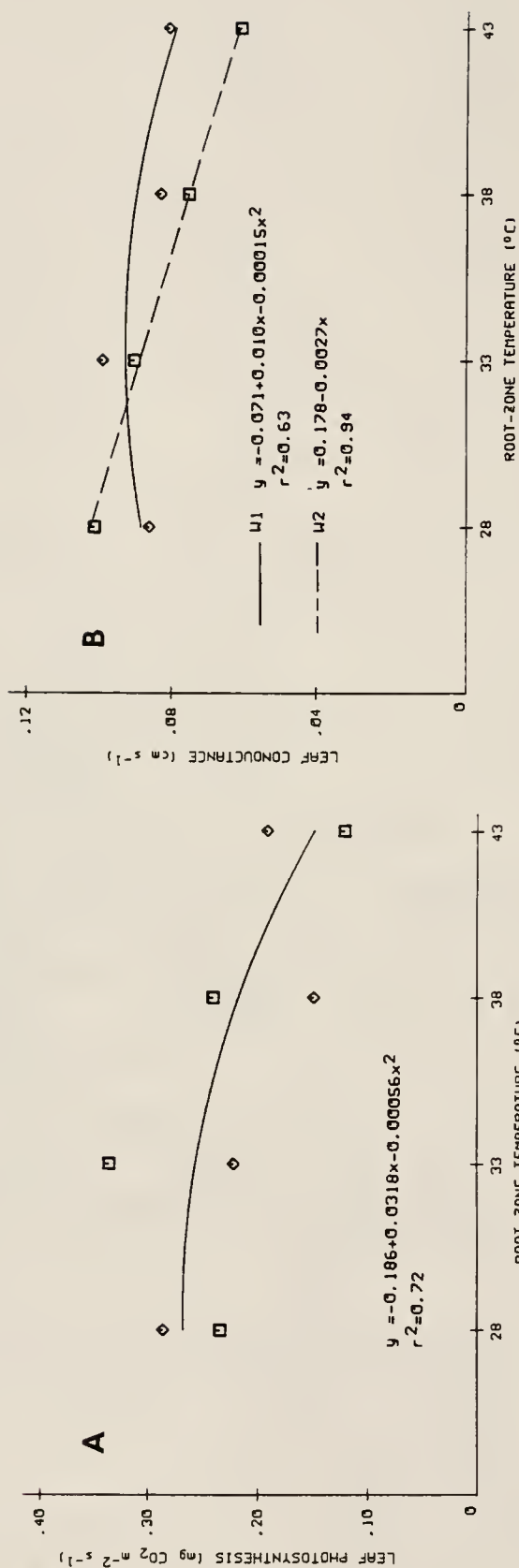


Figure 5-4. Regressions of midday physiological responses of container-grown 'Grande Naine' banana over four root-zone temperatures and two irrigation volumes under greenhouse conditions. Main effects of root-zone temperature on leaf photosynthesis are presented in A and interactive effects of root-zone temperature and irrigation volume on leaf conductance, transpiration and leaf water potential are presented in B, C and D, respectively. W1 (\diamond) = 50 ± 5 ml, W2 (\square) = 100 ± 10 ml daily per 555 cm^3 container.



shifts in CS and TR, there might have been a RZT-induced delay in stomatal opening in the morning hours.

There were significant interactions between irrigation treatments and RZT on midday CS, TR and LWP (Figure 5-4B, 5-4C, 5-4D). For plants under the W1 irrigation level, a quadratic trend was observed for CS and TR. CS and TR were generally increased by the 33°C RZT compared to the other RZTs. At the W2 irrigation level, TR and CS decreased linearly with increasing RZT.

Irrigation treatments altered the influence of RZT on midday LWP with the W2 level resulting in higher LWPs at all RZTs except in plants exposed to the 28°C treatment (Figure 5-4D). RZTs above 28°C, increased plant water status under well-watered conditions but a corresponding increase in gas exchange processes did not occur. This suggested a direct effect on stomatal opening by high RZTs which was not influenced by LWP.

Growth responses--banana. Plant height, stem diameter, leaf length and leaf number did not differ with RZT or irrigation treatments but width and area of the third newest leaf were significantly reduced by RZT (Table 5-1). Effects of the 43°C RZT became evident as early as two weeks after initiation of treatments (Figure 5-5) with induced reductions in leaf area expansion by the 38° and 43°C RZTs occurring

Table 5-1. Growth components of 'Grande Naine' banana measured after 10 weeks at four root-zone temperatures and two irrigation volumes under greenhouse conditions.

Stress treatments	Plant height (cm)	No. of leaves	Stem diam. (cm)	Leaf ^Z length (cm)	Leaf ^Z width (cm)	Leaf ^Z area (cm ²)
RZT (°C)						
28	44.0	11.6	2.6	23.7	10.1	155.9
33	43.6	11.5	2.4	22.8	10.5	155.7
38	43.2	11.9	2.6	23.3	09.8	148.4
43	43.7	12.2	2.6	21.2	09.2	126.7
Irrigation volume (IRV)						
W1 ^Y	42.6	11.6	2.6	22.6	09.9	145.4
W2	44.2	11.8	2.5	22.9	09.8	145.9
Significance ^X						
RZT	NS	NS	NS	NS	Q*	Q*
IRV	NS	NS	NS	NS	NS	NS

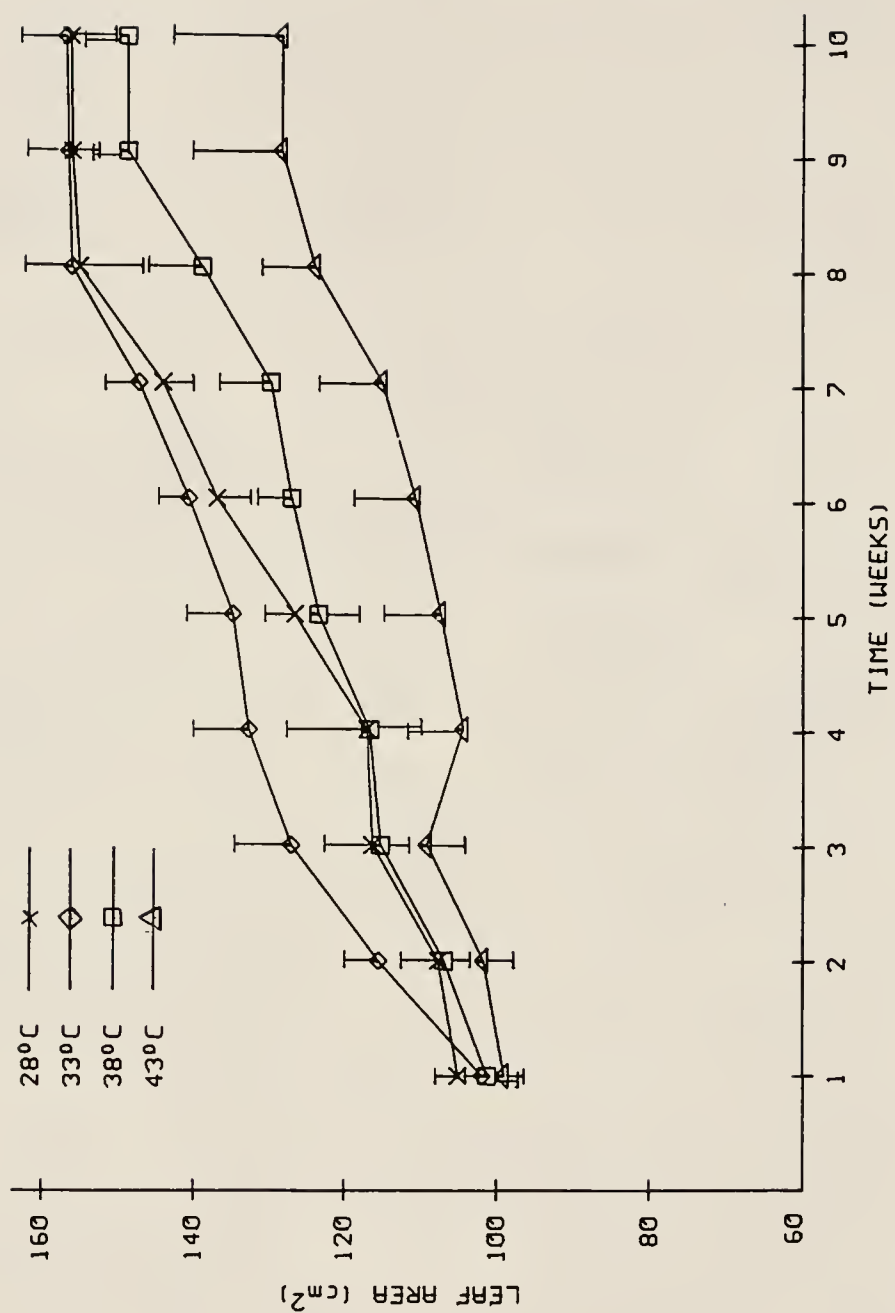
^ZMeasurements taken on the third newest leaf.

^YW1 - 50±5 ml, W2 - 100±10 ml per container daily.

^XStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Quadratic (Q).

*, NS - significant at the 5% probability level and nonsignificant, respectively .

Figure 5-5. Effects of four root-zone temperatures across two irrigation volumes (50+5 ml and 100+10 ml daily per 555 cm³ container) on leaf area of the third newest leaf in container-grown 'Grande Naine' banana measured over 10 weeks under greenhouse conditions. Points are the means of six replicate plants and vertical bars represent the SE.



throughout the experiment. At 10 weeks the effects of the high RZTs on leaf area were being moderated since many roots were growing at or above the soil level of the containers and escaping RZT treatments. Regression analysis of final leaf area with RZT indicated a quadratic relationship ($y = -52.26 + 13.497x - 0.217x^2$; $r^2 = 0.97$) with reductions in leaf area at the 38° and 43°C RZTs without irrigation effects (Table 5-1). Reductions in leaf width was the major contributor to reductions in leaf area.

Shoot, stem and total plant dry weights were not influenced by RZT or irrigation treatments (Table 5-2). However, effects of RZT on root dry weight and thus shoot/root ratio were altered by irrigation treatments (Figure 5-6A, 5-6B). The general RZT-induced increase in root dry weight of the greenhouse-grown banana plants appeared to contradict the decrease in root weight expected under similar RZT treatments (30,39,44,65). By the end of the 10-week experiment, plants were somewhat pot-bound and roots of plants exposed to the higher RZTs were located mainly in the upper portion of the container. Due to the gradient of +1.0°C within containers, as noted previously, these roots may have been exposed to the lower limits of each RZT treatment.

Regression analyses indicated that root dry weight was increased by the 38° and 43°C RZTs under the W1 treatment but only by the 38°C RZT in the W2 treated plants (Figure 5-6B). The 43°C RZT in the W2 treatments could have disrupted the absorptive capacity of banana roots thus creating a flooding-

Table 5-2. Dry weight components of 'Grande Naine' banana measured after 10 weeks at four root-zone temperatures and two irrigation volumes under greenhouse conditions.

Stress treatments	Stem dry wt (g)	Shoot dry wt (g)	Total plant dry wt (g)
RZT (°C)			
28	14.4	20.1	25.8
33	12.9	17.9	23.7
38	14.2	20.3	29.3
43	12.9	18.5	25.9
Irrigation volume (IRV)			
W1 ^z	13.7	19.3	26.5
W2	13.6	19.1	24.9
Significance ^y			
RZT	NS	NS	NS
IRV	NS	NS	NS

^zW1 - 50±5 ml, W2 - 100±10 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons.

NS - nonsignificant at the 5% probability level.

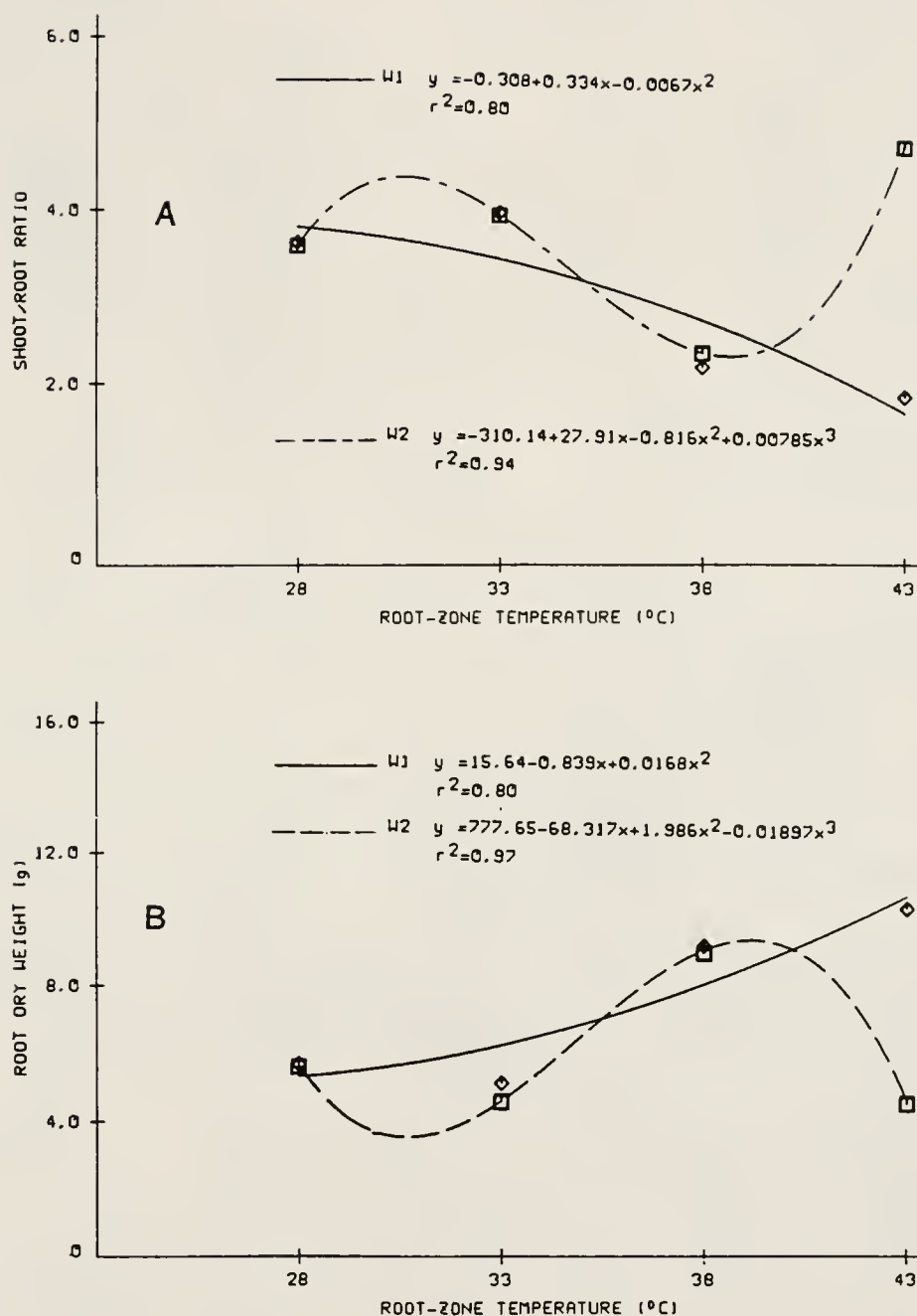


Figure 5-6. Effects of four root-zone temperatures and two irrigation volumes on A. shoot/root ratio and B. root dry weight of container-grown 'Grande Naine' banana under greenhouse conditions. W1 (\diamond) = 50+5 ml, W2 (\square) = 100+10 ml per 555 cm³ container daily. Points are irrigation treatment means.

like situation under the high irrigation treatment and resulting in restricted root growth. A similar condition was reported for well-watered container-grown eggplants (Solanum melongena L.) grown at 40°C RZT which resulted in decreased root dry weight (118).

Root morphology was also influenced. Roots were lacking distinct tips and were brown and less succulent in plants at the 38° and 43°C RZTs than at the lower RZTs. Suberization of roots at high RZT (22° to 35°C) was observed in ryegrass (Poa pratensis L.) (32), peach (Prunus persica Batch.) (99), and rose (Rosa sp. L.) (124).

Carbohydrate analysis--banana. Absolute shoot carbohydrate content was not influenced by stress treatments under greenhouse conditions but there were significant RZT effects on root sugar and shoot sugar/root sugar ratios (Table 5-3). RZT and irrigation volumes also affected root sugar/starch ratio (Figure 5-7). Root sugar content was greatest in plants grown at the 33° and 38°C RZTs. Shoot sugar/root sugar ratios revealed a corresponding decrease by the 33° and 38°C RZT (Table 5-3) and plants treated with these RZTs generally had better water status as reflected by LWP (Figure 5-4D). Increased shoot sugar or shoot sugar/root sugar ratio have been implicated in the process of osmotic adjustment (57,74,105). Sugars not needed for maintaining turgor in plants at the 33° and 38°C RZTs could be available for translocation to the roots thus giving higher root sugar

Table 5-3. Shoot and root carbohydrate distribution in 'Grande Naine' banana measured after 10 weeks at four root-zone temperatures and two irrigation volumes under greenhouse conditions.

Stress treatments	Shoot sugar (% dwt)	Shoot starch (% dwt)	Root sugar (% dwt)	Root starch (% dwt)	SSUG ^z RSUG
RZT (°C)					
28	3.5	3.8	2.0	3.9	2.0
33	3.1	3.4	3.3	3.2	1.0
38	3.0	3.5	3.4	3.5	0.9
43	3.6	3.3	1.5	3.0	2.5
Irrigation volume (IRV)					
W1 ^y	3.3	3.7	2.4	3.7	1.6
W2	3.3	3.3	2.6	3.1	1.5
Significance ^x					
RZT	NS	NS	Q**	NS	Q**
IRV	NS	NS	NS	NS	NS

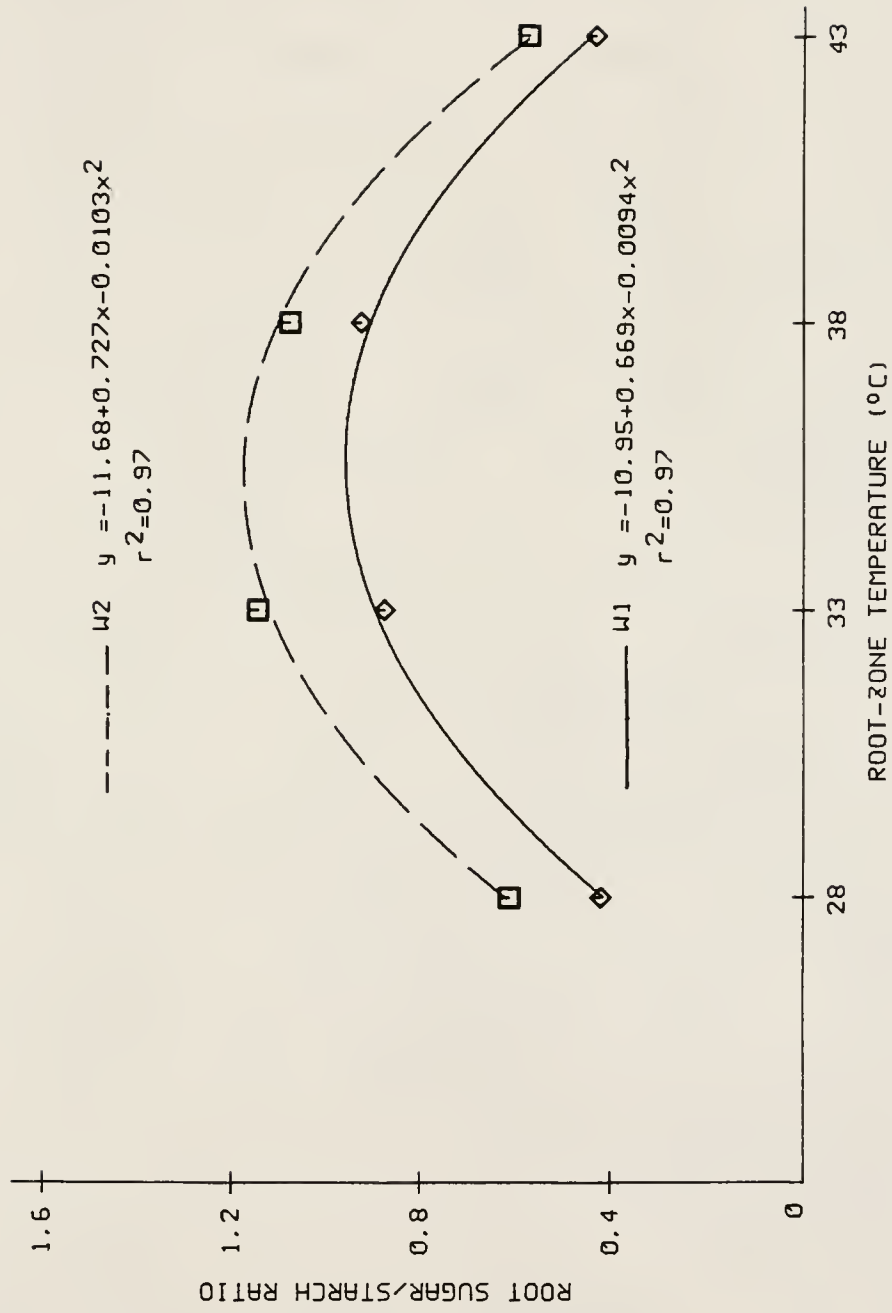
^zSSUG - shoot sugar, RSUG - root sugar.

^yW1 - 50±5 ml, W2 - 100±10 ml per container daily.

^xStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Quadratic (Q).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

Figure 5-7. Effects of four root-zone temperatures and two irrigation volumes on root sugar/starch content of 'Grande Naine' banana grown under greenhouse conditions. $W1 (\diamond) = 50 \pm 5 \text{ ml}$, $W2 (\square) = 100 \pm 10 \text{ ml}$ daily per 555 cm^3 container. Points are irrigation treatment means.



concentrations at these RZTs. Partitioning between sugar and starch in the roots was influenced by irrigation levels with a higher root sugar/starch ratio in the W2 treated plants (Figure 5-7). This agrees with other reports in which increased starch to sugar conversion in the roots occurred under well-watered conditions (106).

Physiological responses--ixora. PS of plants receiving the W1 irrigation volume was generally higher at 1400 and 1600 hr if grown at 33° and 38°C RZTs compared to 28° and 43°C (Figure 5-8A). Maximum CS and TR occurred at midday for the 28°C RZT treated plants and at 1400 hr for plants at the 33° and 38°C RZTs (Figure 5-8B, 5-8C). The 43°C RZT reduced CS and TR at midday and CS at 1400 hr. LWP declined from 1000 hr to midday at the lower irrigation level in plants at the 28°, 33° and 38°C RZTs, but increased to early morning levels by 1600 hr (Figure 5-8D). Midday LWP at 43°C RZT was apparently influenced by midday decreases in CS and TR and did not decline to as low values as the other treatments at midday.

Diurnal patterns of measured parameters in plants under the higher irrigation volume were similar to those under the W1 irrigation treatment. Maximum PS occurred at 1400 hr in the 33°C RZT treated plants and in the 33° and 38°C RZT treated plants at 1600 hr (Figure 5-9A). CS and TR were significantly higher between 1200 and 1400 hr for the 28° and 33°C treated plants compared with the other RZTs

Figure 5-8. Effects of four root-zone temperatures and a 50+5 ml daily irrigation volume per 555 cm³ container on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

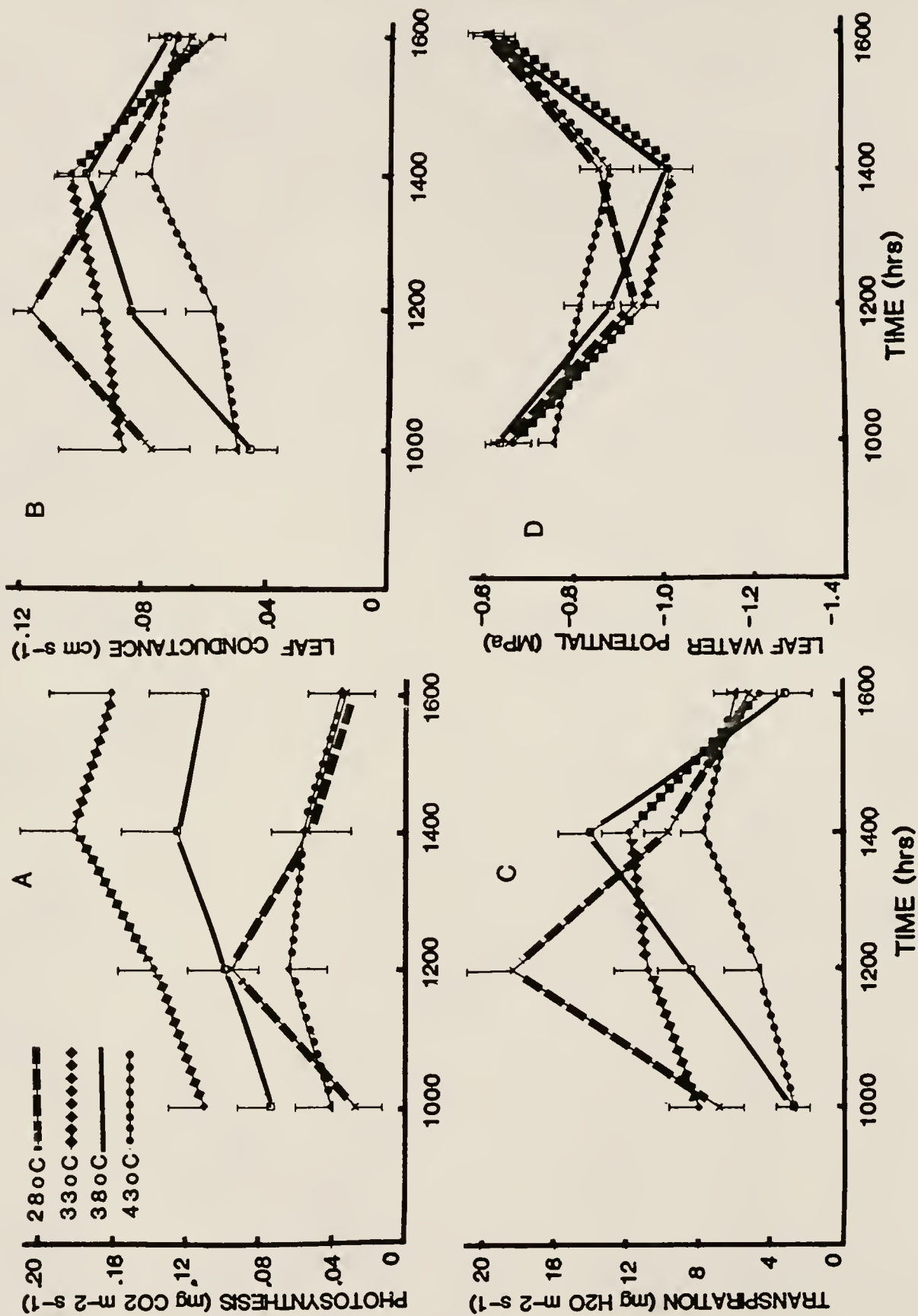
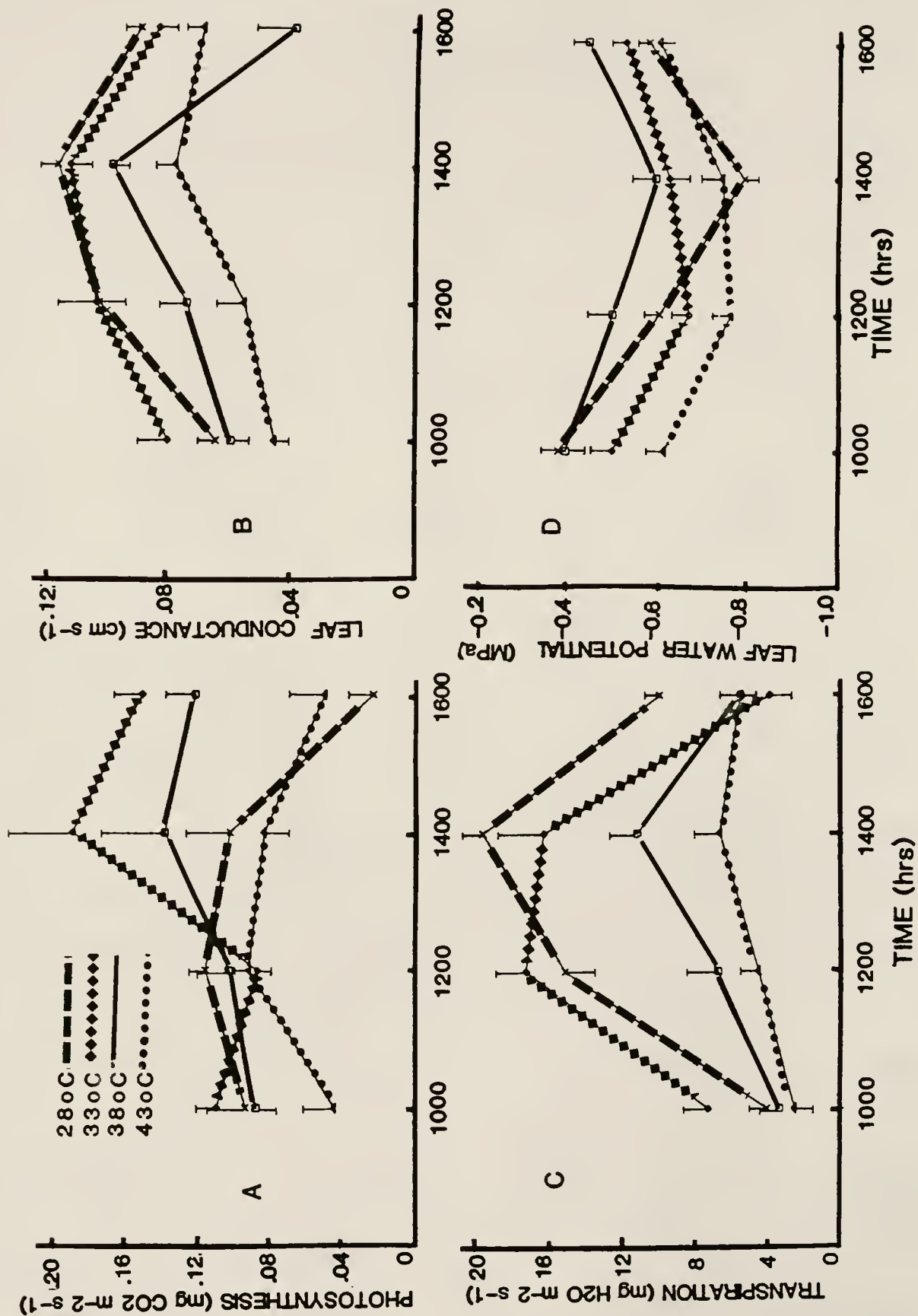


Figure 5-9. Effects of four root-zone temperatures and a 100+10 ml daily irrigation volume per 555 cm³ container on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under greenhouse conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.



(Figure 5-9B, 5-9C). Decreased LWP corresponded to increases in TR and CS at midday and LWP increased as TR and CS declined at 1600 hr (Figure 5-9D). Plants at the 43°C RZT had lowest LWPs at 1000 and 1200 hr and the 38°C RZT treated plants had highest LWP at midday.

Significant effects of RZT on PS, CS and TR were observed when midday values of these parameters were regressed over RZT but irrigation treatments did not alter these effects (Figure 5-10). Quadratic trends occurred for PS and CS with significant decreases at the 43°C RZT (Figure 5-10A, 5-10B) and TR decreased linearly with increasing RZT (Figure 5-10C). Regression analysis for LWP indicated significant interactions of RZT and irrigation treatments (Figure 5-10D). Midday LWP of plants receiving the W2 irrigation treatment were significantly higher than those at the W1 level except at the 43°C RZT (Figure 5-10D). The 43°C RZT, therefore, decreased all measured gas exchange processes at midday in ixora and increased water volume did not improve plant water status. Since the 43°C RZT also appeared supraoptimal after two weeks of RZT stress treatments (Chapter IV), there apparently was little conditioning in ixora to this high RZT.

Growth responses--ixora. Except for axillary shoot number, most growth components and the number of flower buds in the greenhouse-grown plants were significantly affected by RZT but not by irrigation treatments (Table 5-4). While

Figure 5-10. Regressions of midday physiological responses of container-grown *Ixora chinensis* L. 'Maui' over four root-zone temperatures and two irrigation volumes under greenhouse conditions. Main effects of root-zone temperature on leaf photosynthesis, leaf conductance and transpiration are presented in A, B and C, respectively and interactive effects of root-zone temperature and irrigation volume on leaf water potential are presented in D. W1 (\diamond) = 50+5 ml, W2 (\square) = 100+10 ml daily per 555 cm³ container.

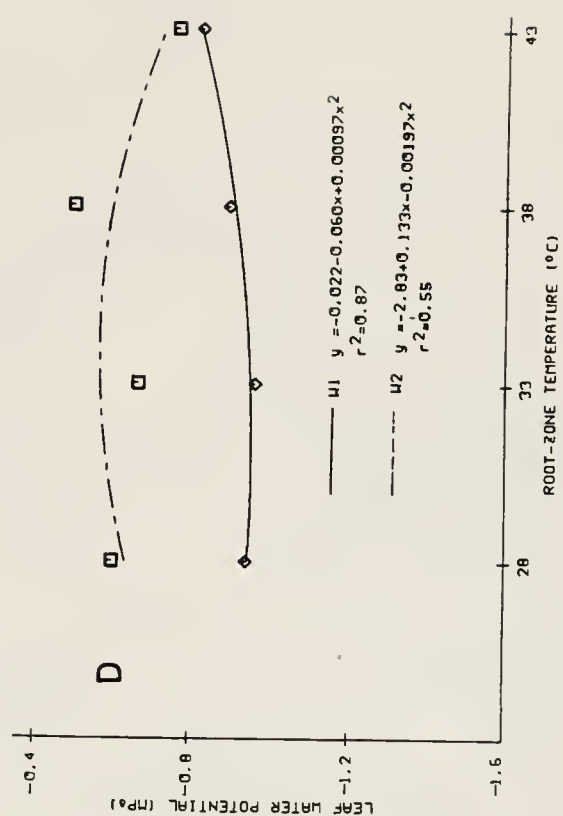
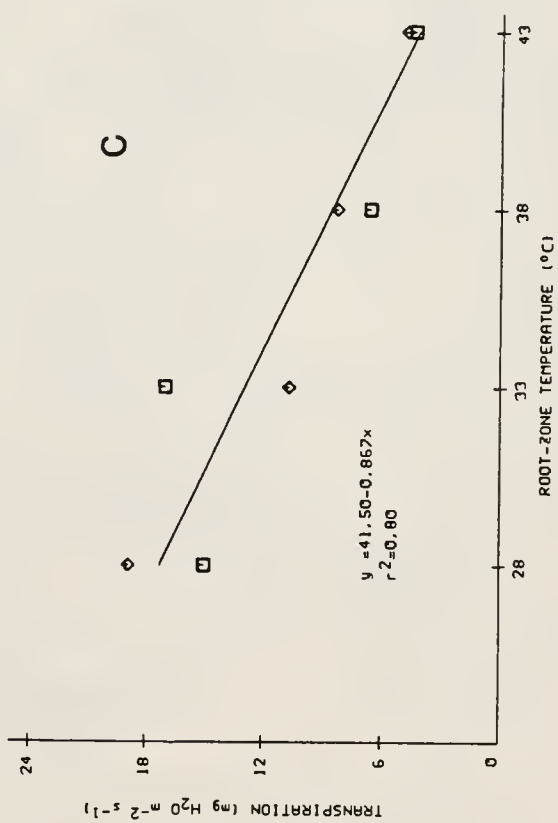
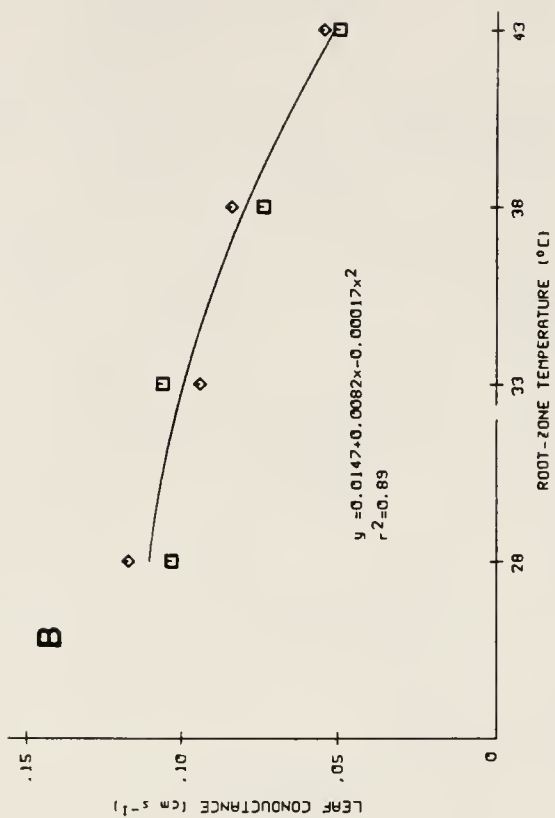
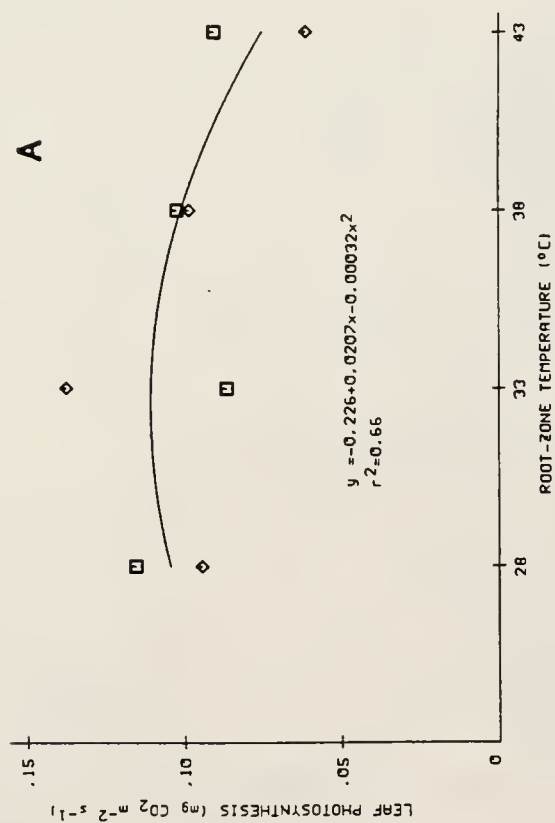


Table 5-4. Growth components of *Ixora chinensis* L. 'Maui' measured after 10 weeks at four root-zone temperatures and two irrigation volumes under greenhouse conditions.

Stress treatments	Plant height (cm)	Plant width (cm)	No. of axillary shoots	Axillary shoot length (cm)	No. of flower buds
RZT ($^{\circ}\text{C}$)					
28	32.5	19.4	2.8	37.3	1.2
33	40.8	24.0	3.2	52.9	0.6
38	43.0	25.2	3.3	61.5	0.2
43	37.1	22.8	2.6	51.2	0.2
Irrigation volume (IRV)					
W1 ^z	39.1	22.5	2.8	50.4	0.6
W2	37.6	23.2	3.1	51.1	0.5
Significance ^y					
RZT	Q**	Q*	NS	Q**	Q**
IRV	NS	NS	NS	NS	NS

^zW1 - 50 \pm 5 ml, W2 - 100 \pm 10 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Quadratic (Q).

**, *, NS - significant at the 1%, and 5% probability levels and nonsignificant, respectively.

growth parameters were increased (Figure 5-11A, 5-11B, 5-11C), flower bud number declined at RZTs above 28°C (Figure 5-11D). Since flowering and subsequent axillary growth occurred in the 28°C treated plants midway in the study, axillary shoot length (Figure 5-11C) but not shoot number (Table 5-4) was significantly different at 10 weeks.

There were interactive effects of RZT and irrigation volume on shoot, total plant and root dry weights (Figure 5-12A, 5-12B, 5-12D) but only RZT effects on shoot/root ratio (Figure 5-12C). Shoot and total plant dry weights increased at RZTs above 28°C under the W2 irrigation level but these parameters were maximum at 38°C RZT under the W1 irrigation treatment (Figure 5-12A, 5-12B). All dry weight parameters were significantly increased by irrigation at the 33°C RZT. While the higher irrigation level overcame the stress effects of the 43°C RZT on shoot and total plant dry weight (Figure 5-12A, 5-12B), it did not increase root dry weight over that in the W1 treated plants at 38° and 43°C RZT (Figure 5-12D).

Larger shoots with reduced roots at the higher RZTs (Figure 5-12C) would imply a RZT-induced increase in root absorption and/or increased assimilate supply. However, trends in TR (Figure 5-10C) and PS (Figure 5-10A) suggested that neither water absorption nor assimilate production was increased in plants at RZTs above 33°C. This leaves the possibility of a RZT-induced increase in hormonal synthesis (64,76,91) and/or export from the roots (91,129) as a cause for the increased axillary shoot growth. An increased

Figure 5-11. Main effects of four root-zone temperatures across two irrigation volumes (50+5 ml and 100+10 ml daily per 555 cm³ container) on growth of Ixora chinensis L. 'Maui' grown under greenhouse conditions. A. plant height B. plant width C. axillary shoot length and D. number of flower buds. Points are the means of 12 replicate plants.

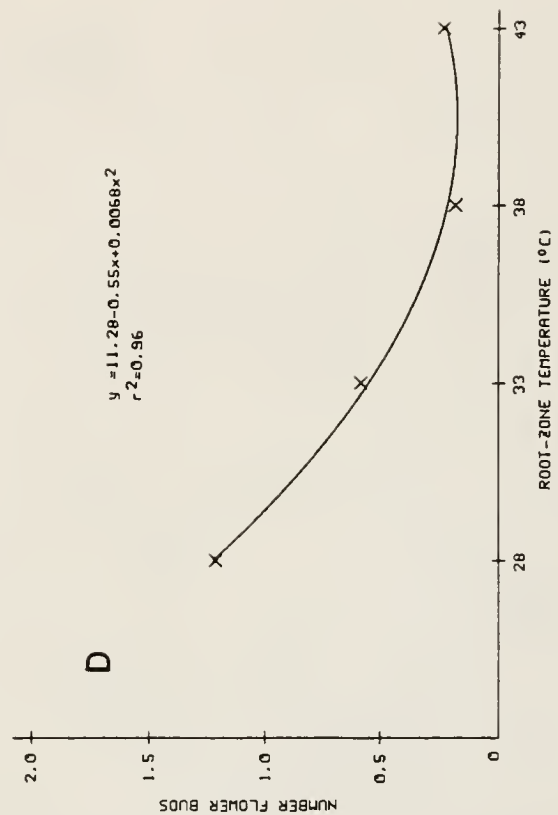
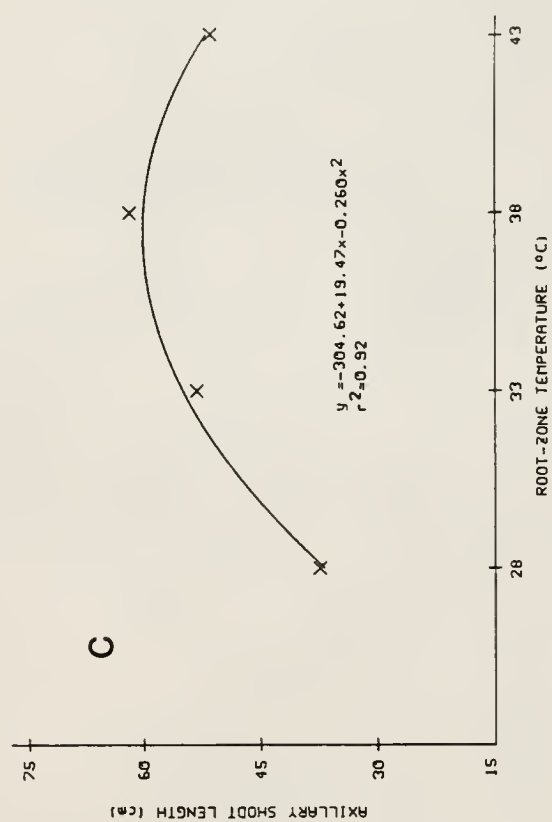
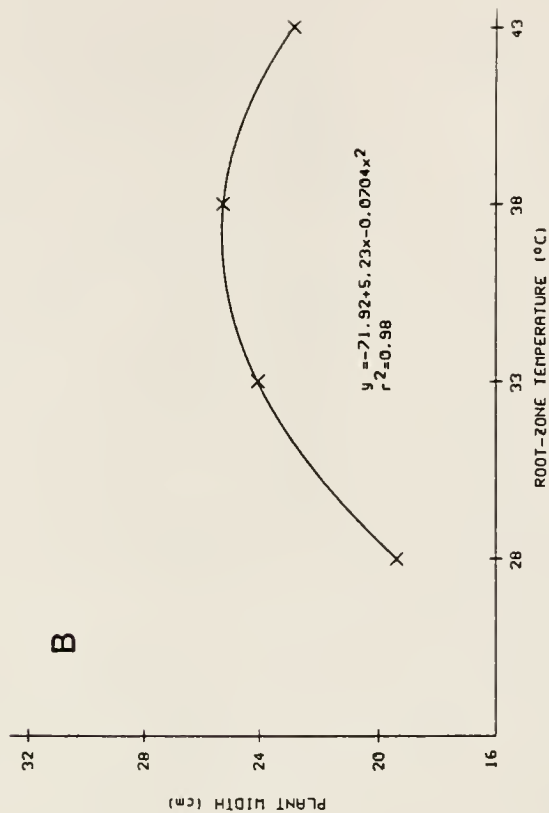
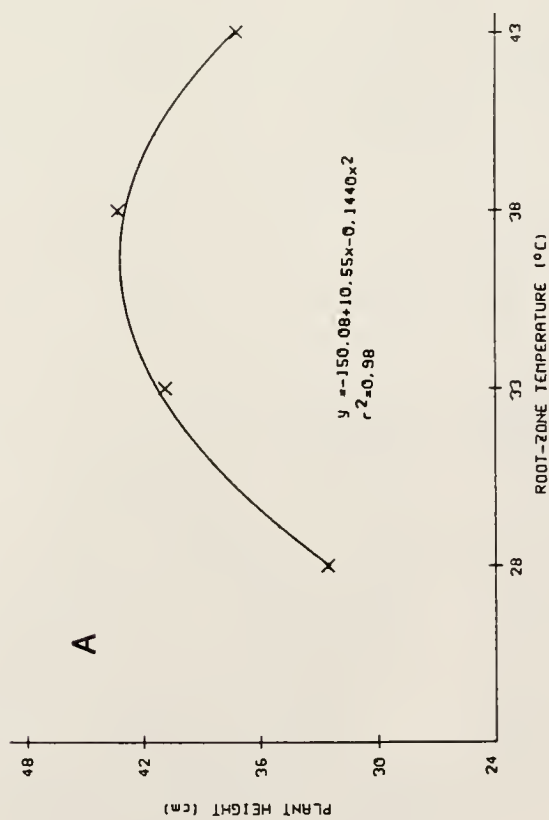
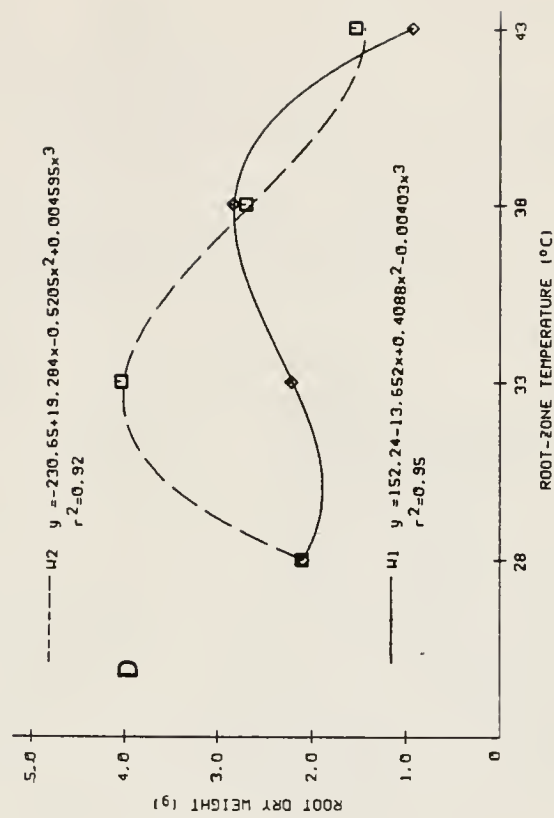
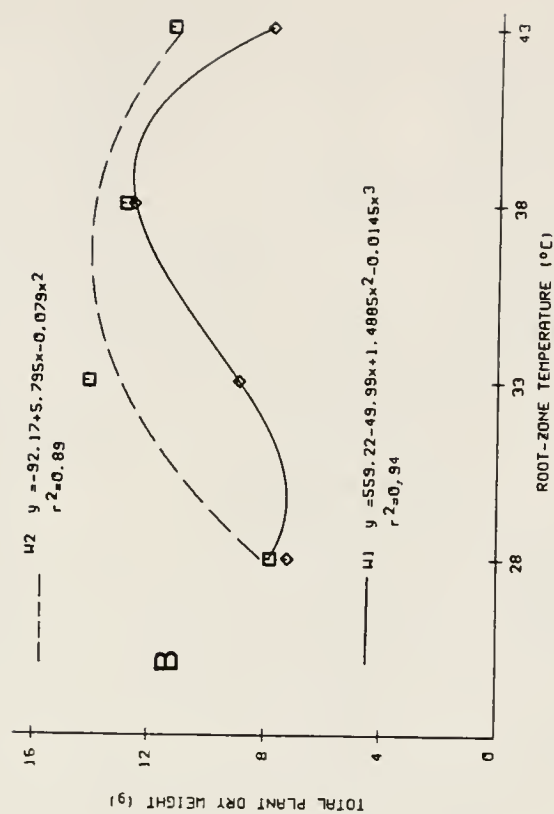
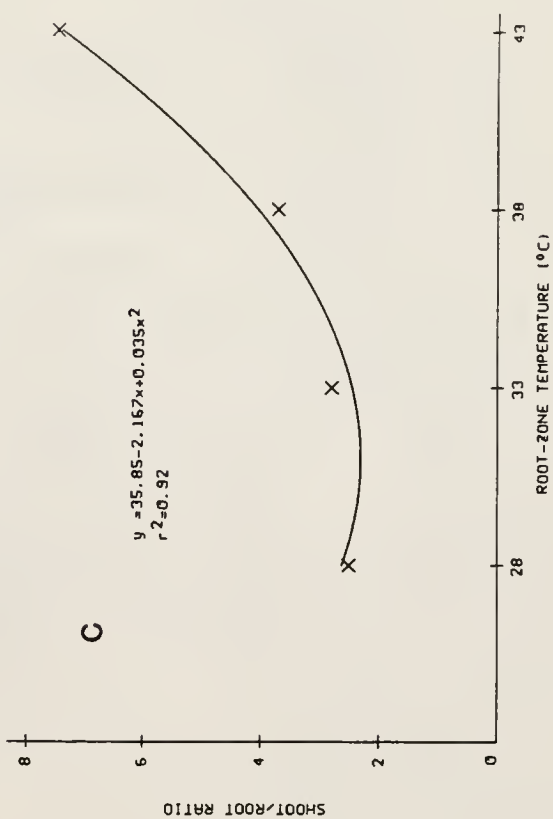
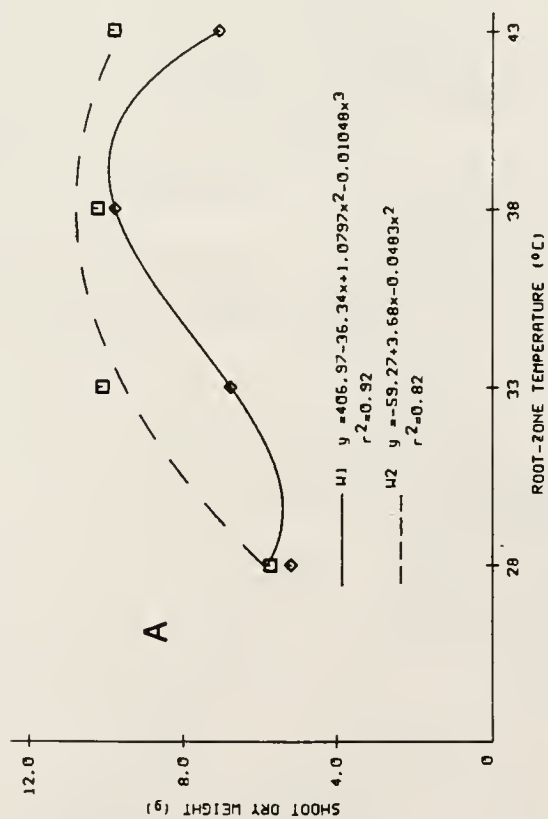


Figure 5-12. Effects of four root-zone temperatures and two irrigation volumes on dry weight components of container-grown Ixora chinensis L. 'Maui' under greenhouse conditions. Interactive effects of root-zone temperature and irrigation volume on shoot dry weight, total plant dry weight and root dry weight are presented in A, B and D, respectively and main effects of root-zone temperature on shoot/root ratio are presented in C. $W1 (\diamond) = 50 \pm 5$ ml, $W2 (\square) = 100 \pm 10$ ml daily per 555 cm³ container. Points represent irrigation treatment means in A, B and D and the means of 12 replicate plants in C.



acropetal flow of root-synthesized cytokinin may be postulated (21,129) since increased axillary shoot growth (Figure 5-11C), apparently at the expense of flowering (Figure 5-11D), was induced by increased RZT.

Carbohydrate analysis--ixora. Absolute shoot sugar and shoot and root starch contents were not affected by RZT or irrigation treatments under greenhouse conditions but root sugar content decreased and thus shoot sugar/root sugar ratio increased linearly with increasing RZT (Table 5-5). These trends in carbohydrate status indicated a maintenance of shoot sugar content with either decreased translocation to the roots (96) or increased respiration in the roots (58) with increasing RZT.

PS did not increase in plants at the 38°C RZT compared to lower RZTs and declined at the 43°C RZT (Figure 5-10A). However, demand for photosynthates in plants at the 38°C and 43°C RZTs would be increased by the increased sink strength of RZT-induced axillary shoot growth. Under these conditions, there would probably be less available soluble sugars for translocation to the roots, hence the decreased root sugar content. Increased root respiration at high RZT with less available substrates could also have contributed to the decreased root dry weight at the 43°C RZT (Figure 5-12B).

Table 5-5. Shoot and root carbohydrate distribution in Ixora chinensis L. 'Maui' after 10 weeks at four root-zone temperatures and two irrigation volumes under greenhouse conditions.

Stress treatments	Shoot sugar (% dwt)	Shoot starch (% dwt)	Root sugar (% dwt)	Root starch (% dwt)	<u>Shoot sugar</u> <u>root sugar</u>
RZT (°C)					
28	4.4	3.2	5.7	3.6	0.8
33	5.9	2.6	3.8	3.5	1.5
38	4.8	2.7	3.8	3.2	1.3
43	5.0	2.7	3.2	2.9	1.6
Irrigation volume (IRV)					
W1 ^z	5.2	2.6	4.1	3.1	1.4
W2	4.9	3.1	4.2	3.5	1.2
Significance ^y					
RZT	NS	NS	L**	NS	L**
IRV	NS	NS	NS	NS	NS

^zW1 - 50⁺5 ml, W2 - 100⁺10 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Linear (L).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

Experiment 2--Growth Room

Physiological responses--banana. Under the W1 irrigation volume, plants at the 38°C RZT generally achieved higher daily PS compared to the other RZTs with maximum PS rates of 0.485 and 0.470 mg CO₂ m⁻² s⁻¹ at 1200 and 1400 hr, respectively (Figure 5-13A). Maximum PS recorded at two weeks (Figure 4-3A, Chapter IV) in the growth room, also occurred in 38°C RZT treated plants. High PS in plants exposed to the 38°C RZT for six weeks under reduced irrigation may suggest that this RZT is within the optimum range for PS in banana. The 43°C RZT resulted in comparatively lower PS at two and six weeks after treatment imposition, indicating that there was no evidence of conditioning to this extreme RZT treatment.

Differences in CS and TR were not discernible between RZTs except for the consistent reductions at midday and 1400 hr in the 43°C treatment. The 28°C RZT-treated plants had significantly higher LWP at 0800 hr and midday.

Under the W2 irrigation level, the 33°C RZT treated plants had relatively higher midday PS than those at other RZTs (Figure 5-14A) and this was related to a correspondingly higher TR at this RZT (Figure 5-14C). CS was significantly reduced at midday and 1400 hr for plants under the 38° and 43°C RZT (Figure 5-14B) and there was a corresponding decrease in TR for the 43°C RZT treated plants (5-14C). These observations suggested an inhibitory effect on stomatal opening by the 43°C RZT regardless of irrigation treatment

Figure 5-13. Effects of four root-zone temperatures and a 75+8 ml daily irrigation volume per 1200 cm³ container on the diurnal physiological responses of container-grown 'Grande Naine' banana under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

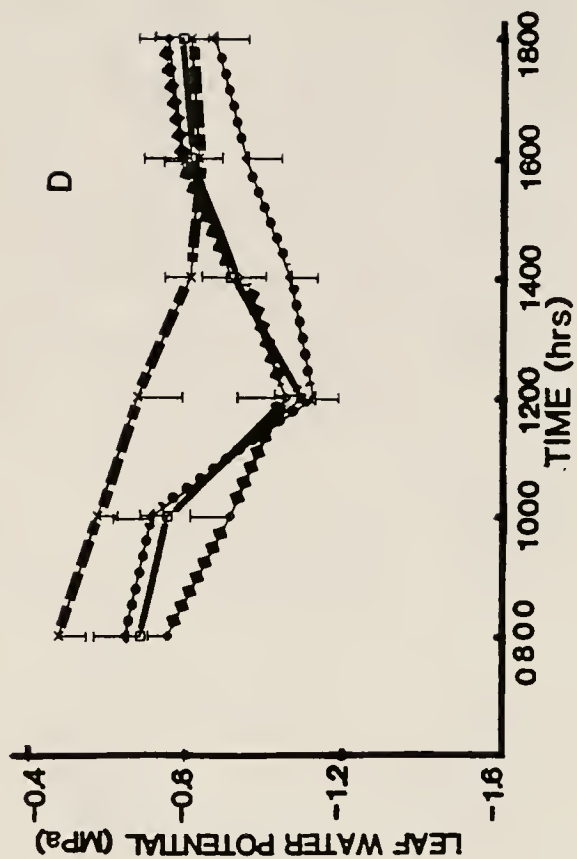
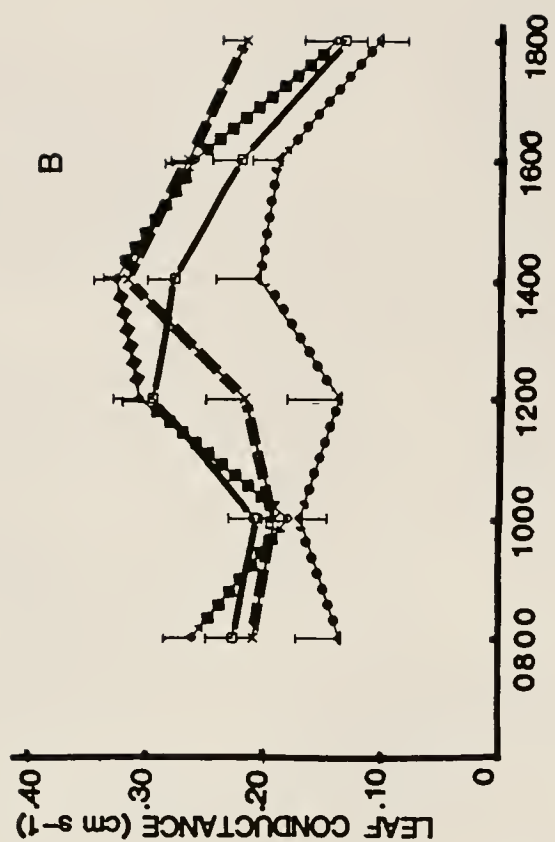
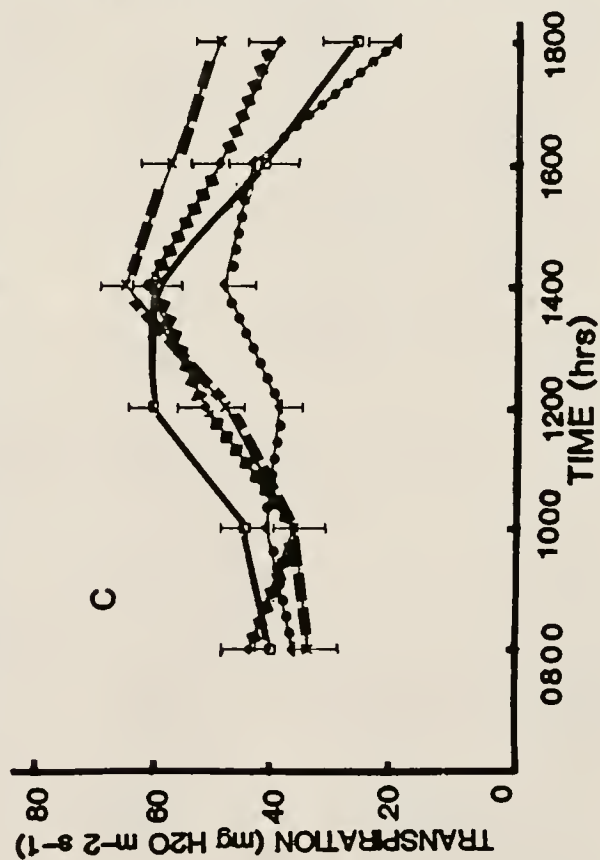
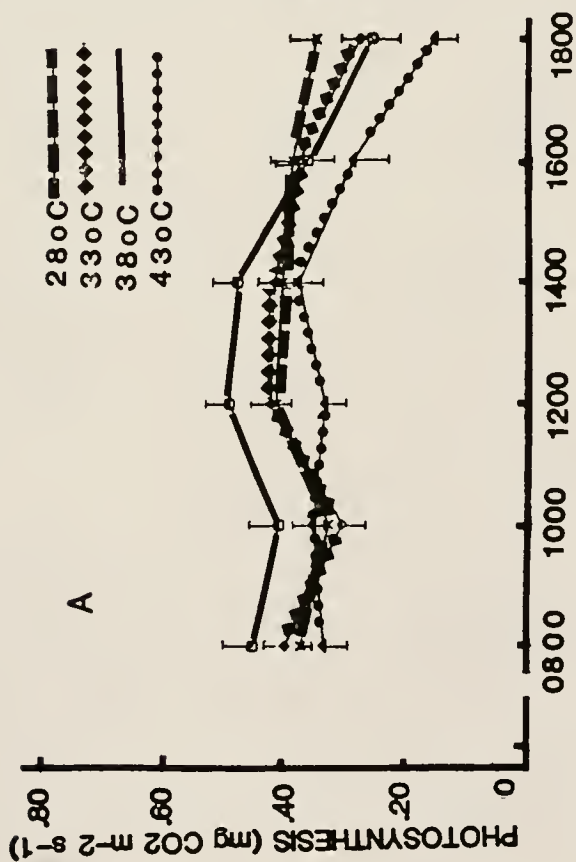
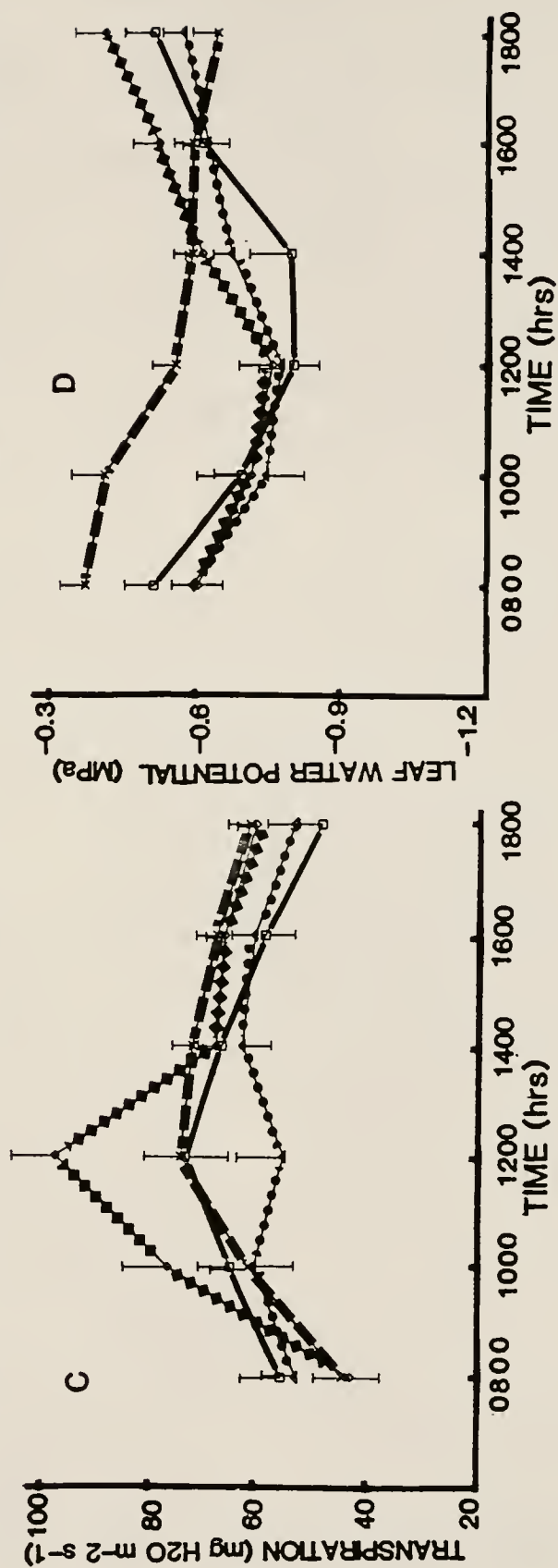
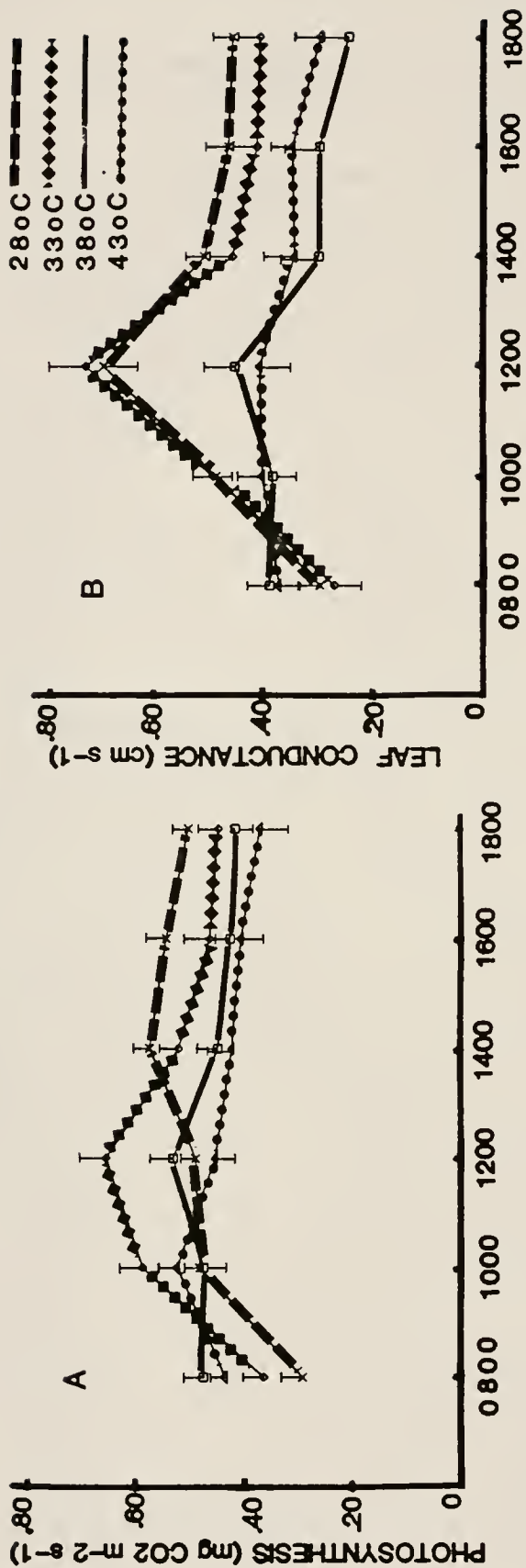


Figure 5-14. Effects of four root-zone temperatures and a 150+15 ml daily irrigation volume per 1200 cm³ container on the diurnal physiological responses of container-grown 'Grande Naine' banana under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

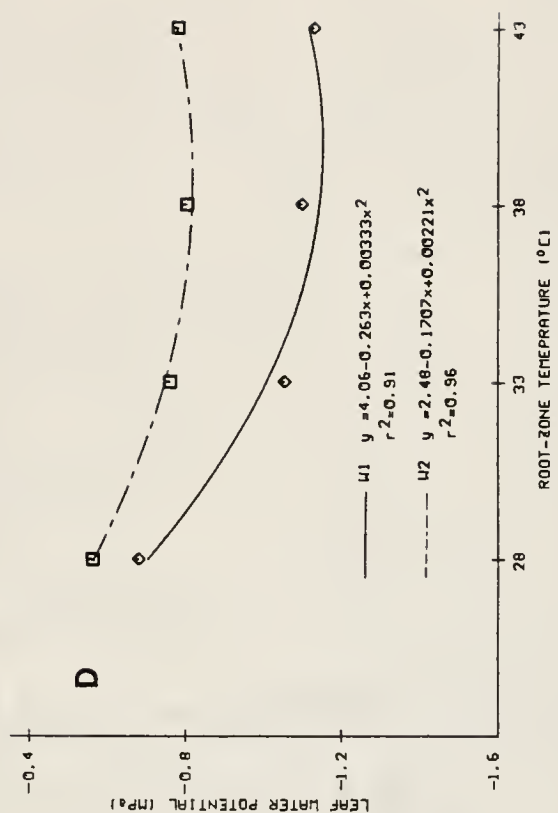
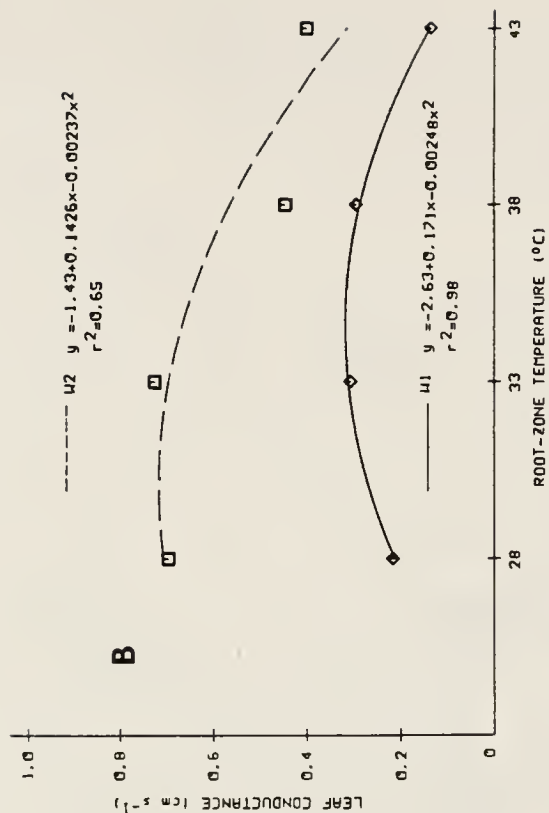
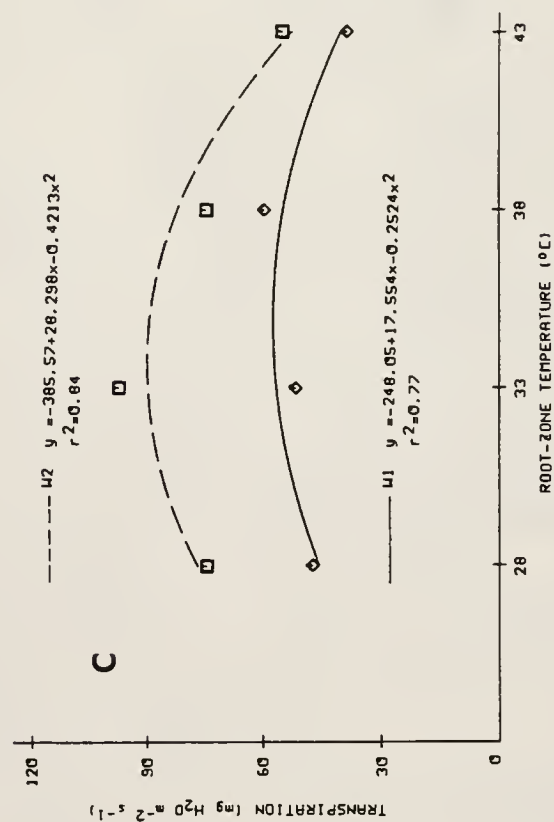
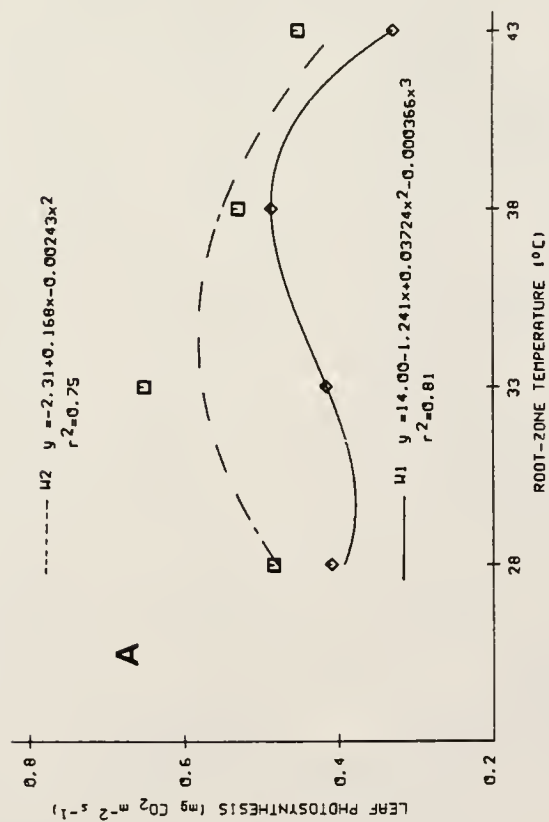


and an inhibition by the 38°C RZT under the higher irrigation level. RZTs above 28°C RZT reduced LWP during the morning hours and increased irrigation did not appear to alter this effect (Figure 5-13D, 5-14D).

Regression analyses of midday PS, CS and TR showed significant effects of RZT and irrigation treatments (Figure 5-15). Maximum midday PS was recorded in plants at the 33°C RZT under the W2 irrigation level with the 38° and 43°C RZT treated plants having midday PS similar to that at 28°C. The maximum midday PS in plants under the W1 irrigation was recorded at 38°C RZT but this was 20% lower than PS in plants at W2 and 33°C RZT (Figure 5-15A). RZT and irrigation interactions also occurred for CS and TR with significant increases under the W2 irrigation at the 28° and 33°C RZTs (Figure 5-15B, 5-15C). RZTs above 28°C generally decreased LWP, but increased irrigation increased LWP except at the 28°C RZT (Figure 5-15D). The positive effect of increased irrigation on LWP at 38° and 43°C RZT but not on the gas exchange processes is somewhat anomalous. As noted previously there may have been some direct RZT effect on stomatal opening at these RZTs independent of leaf water status.

Under growth room conditions, irrigation and RZT interactions indicated that if growth medium temperature for banana is maintained at 33°C, increased irrigation may be beneficial. At 38°C, increased watering may increase plant water status but not necessarily net carbon balance.

Figure 5-15. Regressions of midday physiological responses of container-grown 'Grande Naine' banana over four root-zone temperatures and two irrigation volumes under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. $W1 (\diamond) = 75 \pm 8 \text{ ml}$, $W2 (\square) = 150 \pm 15 \text{ ml}$ daily per 1200 cm^3 container. Points are irrigation treatment means.



Increased irrigation, however, moderates the effect of the 43°C RZT on gas exchange processes.

Growth responses--banana. Plant height, leaf number and leaf length were not affected by RZT or irrigation treatments but stem diameter was increased and leaf width and area were decreased by increasing RZT under growth room conditions (Table 5-6). The effects of RZT on leaf width and area were generally similar to those that occurred in the greenhouse study, although these parameters were linearly reduced by RZT here as compared to the curvilinear relationship in the greenhouse plants.

Dry weights were not altered by RZT or irrigation volumes except for root dry weight and thus shoot/root ratio which were affected by stress treatments with no interactive treatment effects (Table 5-7). Root dry weight was reduced linearly by increasing RZT with the lower irrigation volume causing additional reduction. These results are in general agreement with findings of high RZT on root growth in several plants (30,39,44,65). The greater volume of the RHTs used in this study compared to the containers used in the greenhouse experiment was apparently more adequate for studying RZT stress effects in banana plants. Root tips of plants at the higher RZTs were absent and roots appeared more fibrous and were less succulent at the higher RZTs than at 28° and 33°C RZT. Stunting and browning effects on roots by high RZT has been observed in rye grass (32), peach (99), and rose (124).

Table 5-6. Growth components of 'Grande Naine' banana measured after six weeks at four root-zone temperatures and two irrigation volumes under growth room conditions.

Stress treatments	Plant height (cm)	No. of leaves	Stem diam. (cm)	Leaf ^Z length (cm)	Leaf ^Z width (cm)	Leaf ^Z area (cm ²)
RZT (°C)						
28	37.7	10.0	2.2	21.3	9.9	137.4
33	39.1	10.2	2.5	20.7	9.9	133.5
38	36.5	9.9	2.8	20.9	8.4	114.5
43	36.2	9.8	3.2	20.7	8.2	110.5
Irrigation volume (IRV)						
W1 ^Y	36.7	9.8	2.6	21.1	9.3	127.4
W2	37.7	10.2	2.7	20.8	9.0	122.0
Significance ^X						
RZT	NS	NS	L**	NS	L**	L**
IRV	NS	NS	NS	NS	NS	NS

^ZMeasurements taken on the third newest leaf.

^YW1 - 75±8 ml, W2 - 150±15 ml per container daily.

^XStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Linear (L).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

Table 5-7. Dry weight components of 'Grande Naine' banana measured after six weeks at four root-zone temperatures and two irrigation volumes under growth room conditions.

Stress treatments	Stem dry wt (g)	Shoot dry wt (g)	Root dry wt (g)	Shoot/root ratio	Total plant dry wt (g)
RZT (°C)					
28	10.5	17.9	7.6	2.4	25.6
33	10.2	19.7	6.4	3.1	26.1
38	10.7	18.7	5.3	3.5	24.0
43	10.2	19.9	4.1	5.0	24.0
Irrigation volume (IRV)					
W1 ^z	10.1	18.4	5.0	3.9	23.6
W2	10.9	19.4	6.8	3.0	26.0
Significance ^y					
RZT	NS	NS	L**	L**	NS
IRV	NS	NS	L**	NS	NS

^zW1 - 75±8 ml, W2 - 150±15 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Linear (L).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

As in the greenhouse experiment (Table 5-1, Figure 5-5), leaf area was also decreased by the higher RZTs in this study and the trend in reduction paralleled that of leaf width (Table 5-6). There were also no RZT effects on plant height, which is basically a measure of total leaf length in the banana plant. Anatomical studies revealed that the unfolding banana leaf increases in width mainly through expansion of groups of meristematic cells still evident within the leaf lamina (130). These observations suggested a RZT-induced effect on cell expansion and/or division rather than on cell elongation.

Inhibition of leaf expansion by the 38° and 43°C RZT treatments could have involved physiological mechanisms not entirely associated with leaf water deficits. De Langhe et al. (34), working on endogenous hormonal patterns in developing banana plants, demonstrated that the root tips were a major source of cytokinins in banana plants. Reduced leaf expansion simultaneous with the loss of root tips observed in the high RZT-treated plants under both environmental conditions may imply a hormonal role in leaf expansion. Since leaf width and not leaf length was affected by high RZT, it may be hypothesized that root-synthesized cytokinin was limiting in plants subjected to the 38° and 43°C RZTs. This could be validated in future studies by the application of exogenous cytokinin to high RZT-treated plants and monitoring the effects on leaf expansion.

Leaf chlorophyll content as measured by light absorbance increased linearly with increasing RZT but was not affected by irrigation treatment (Figure 5-16). Increased chlorophyll content however, did not relate to increased PS (Figure 5-15A), thus chlorophyll density may not have increased. Leaf area was affected but dry weight was not altered by RZT. These observations may suggest that a smaller but thicker leaf was produced in response to high RZT.

Carbohydrate analysis--banana. Under the growth room environment, root starch content decreased with increasing RZT (Table 5-8) and there were interactive effects of RZT and irrigation treatments on root sugar and root sugar/starch ratio (Figure 5-17). Regression analysis indicated that root sugar concentration decreased linearly with RZT at the W1 irrigation level but was curvilinearly related to RZT at W2 (Figure 5-17A). RZTs above 28°C generally decreased LWP (Figure 5-15D) thus possibly increasing the demand for soluble sugars in the shoots for osmotic adjustment and leaving less for translocation to the roots. Higher irrigation moderated the RZT stress effects at 43°C (Figure 5-15) and roots were apparently not damaged. A high sink demand of roots under this RZT and the W2 level could have caused the noted root sugar content increase compared to the 33° and 38°C RZTs even under comparable LWPs.

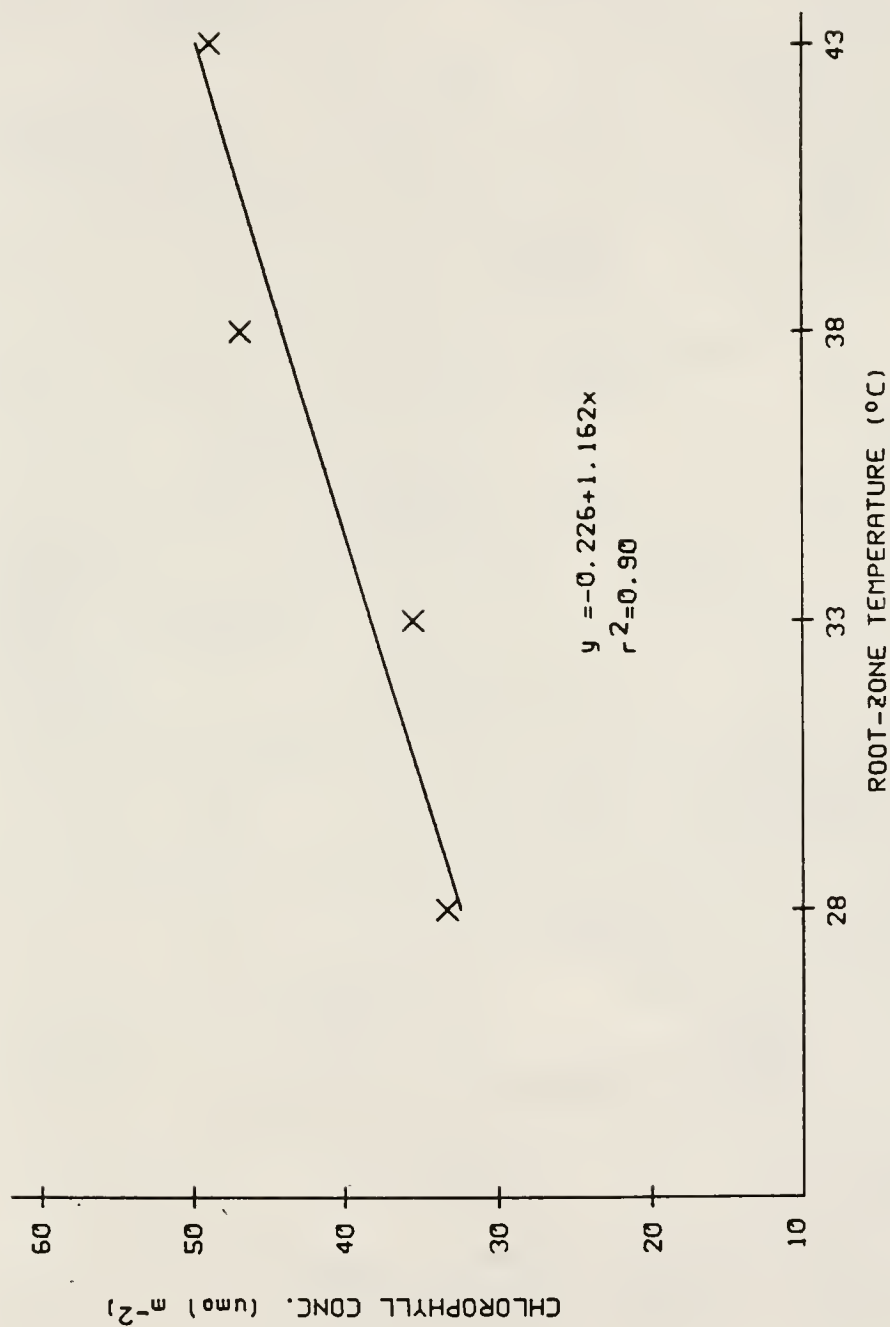


Figure 5-16. Effects of four root-zone temperatures across two irrigation volumes (75+8 ml and 150+15 ml daily per 1200 cm³ container) on chlorophyll concentration of container-grown 'Grande Naine' banana under growth room conditions. Points are the means of 12 replicate plants.

Table 5-8. Shoot and root carbohydrate distribution in 'Grande Naine' banana measured after six weeks at four root-zone temperatures and two irrigation volumes under growth room conditions.

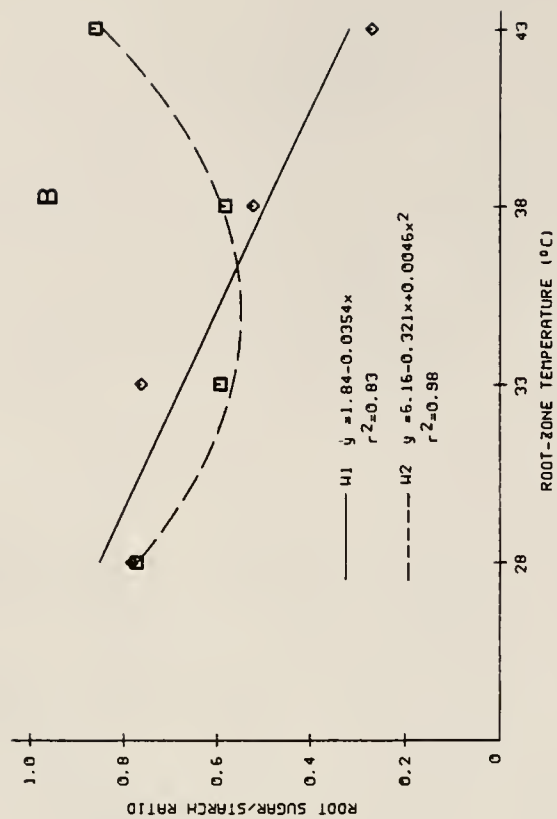
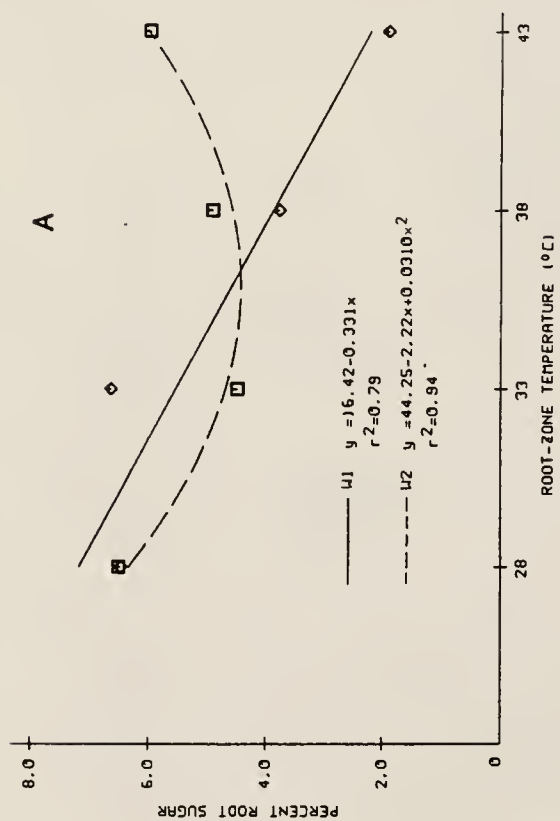
Stress treatments	Shoot sugar (% dwt)	Shoot starch (% dwt)	Root starch (% dwt)	<u>Shoot sugar</u> <u>root sugar</u>
RZT (°C)				
28	4.9	4.9	8.3	0.8
33	4.0	4.4	8.0	0.7
38	4.0	4.6	7.7	0.9
43	3.7	4.0	6.8	1.1
Irrigation volume (IRV)				
W1 ^Z	3.9	4.3	7.6	1.0
W2	4.3	4.7	7.8	0.8
Significance ^Y				
RZT	NS	NS	L**	NS
IRV	NS	NS	NS	NS

^ZW1 - 75±8 ml, W2 - 150±15 ml per container daily.

^YStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Linear (L).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

Figure 5-17. Interactive effects of four root-zone temperatures and two irrigation volumes on carbohydrate content of container-grown 'Grande Naine' banana under growth room conditions. A. percent root sugar and B. root sugar/starch ratio. W1 (\diamond) = 75 ± 8 ml, W2 (\square) = 150 ± 15 ml daily per 1200 cm³ container. Points are irrigation \times treatment means.



Partitioning trends between sugar and starch in the roots were affected by irrigation treatments (Figure 5-17B). Well-watered conditions have been implicated in the interconversion of starch to sugar in roots (107). The expected increase in sink strength at higher RZT and the effect of irrigation may have been responsible for the quadratic trend in root sugar/starch under the W2 irrigation treatment and the linear decrease in the W1 treated plants. Starch content was linearly reduced with increasing RZT irrespective of irrigation treatment (Table 5-8), reflecting possible root starvation effects and the RZT-induced decrease in root dry weight (Table 5-7).

Carbohydrate status and partitioning in banana appeared to be related with RZT-induced changes in plant water status. Turner and Lahav (142) reported significant shifts in assimilate partitioning in banana plants subjected to increasing air temperatures under growth room conditions. In their study, however, neither LWP nor carbohydrate content were measured and their results were based entirely on dry weight determinations. Relating LWP with plant carbohydrate status is probably a more direct method of explaining RZT-induced shifts in partitioning patterns.

Physiological responses--ixora. PS rates were generally higher in the growth room than in the greenhouse. However, diurnal PS patterns were not greatly affected by RZT under the W1 irrigation level in the growth room, except for the

reduced midday rates for the 43°C RZT treated plants (Figure 5-18A). This general pattern was also evident for CS (Figure 5-18B) and TR except that midday TR was also reduced by the 38°C RZT (Figure 5-18C). LWP appeared to be influenced by RZT and its effects on CS and TR. Transpirational water loss did not reduce LWP at 28°C RZT compared to that in plants grown at 33° and 38°C RZTs (Figure 5-18D). The 43°C RZT inhibited stomatal opening directly but apparently did not reduce the absorptive capacity of the roots thus resulting in LWP comparable to that in the 28°C RZT treated plants. Under the W2 irrigation, effects of RZT on diurnal fluctuations were less apparent than in plants with the lower irrigation volume (Figure 5-19), but the 43°C RZT resulted in reduced PS and decreased CS and TR at 1000 hr through midday.

There were no interactive effects of RZT and irrigation treatments on midday PS, CS and TR but quadratic relationships with RZT were noted (Figure 5-20A, 5-20B, 5-20C). RZTs of 28°, 33° and 38°C resulted in similar midday PS, CS and TR but there were discernible reductions for plants at 43°C. This pattern of RZT effects on gas exchange parameters was also apparent in plants in the greenhouse study (Figure 5-10). Regression curves were not presented for responses to RZT in the two week growth room stress study (Chapter IV), but midday values of PS, CS and TR indicated a similar trend as occurred at six weeks. These results suggested that there was little conditioning in ixora to the

Figure 5-18. Effects of four root-zone temperatures and a 75+8 ml daily irrigation volume per 1200 cm³ container on the diurnal physiological responses of *Ixora chinensis* L. 'Maui' grown under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

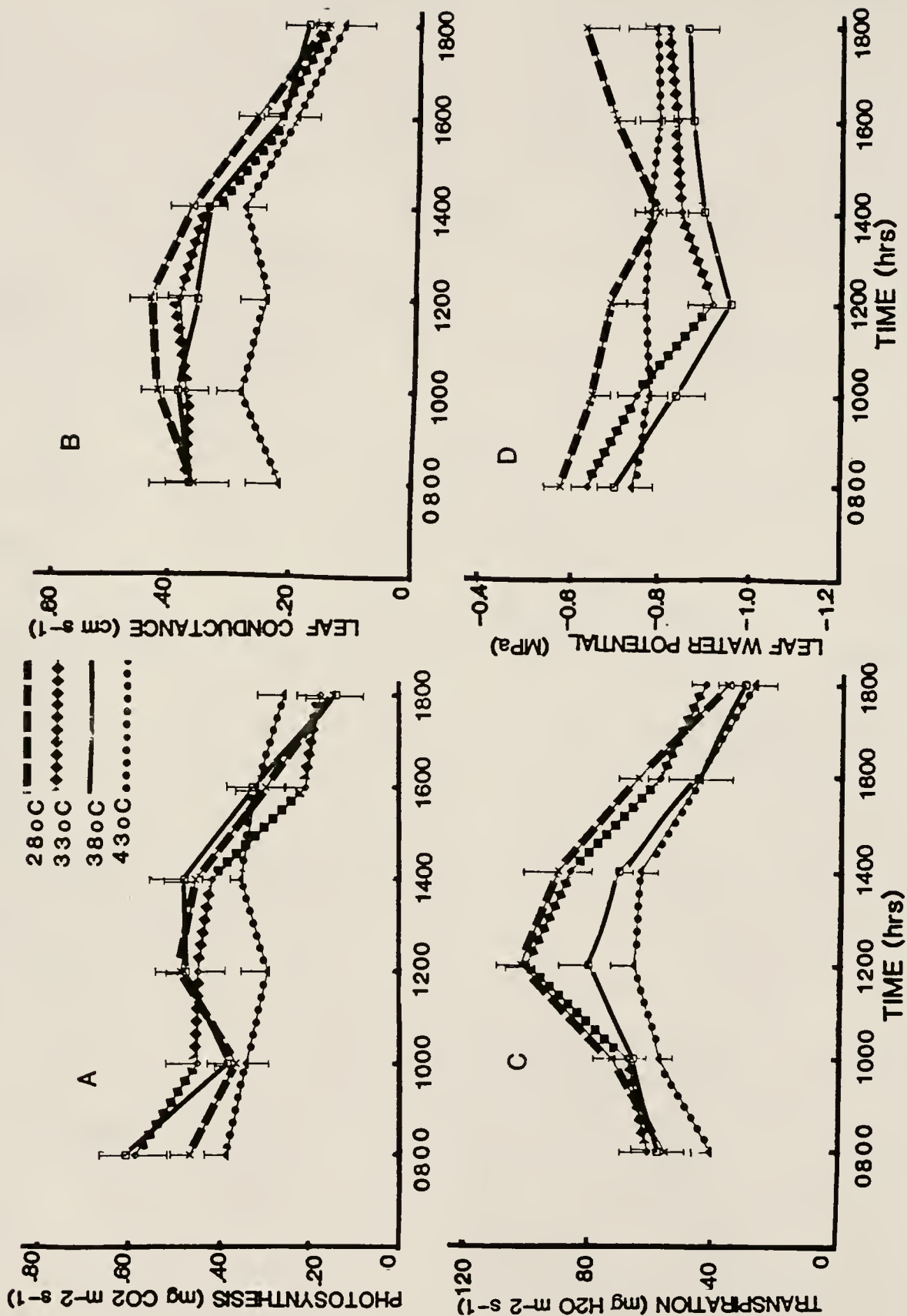


Figure 5-19. Effects of four root-zone temperatures and a 150+15 ml daily irrigation volume per 1200 cm³ container on the diurnal physiological responses of Ixora chinensis L. 'Maui' grown under growth room conditions. A. leaf photosynthesis B. leaf conductance C. transpiration and D. leaf water potential. Points are the means of six replicate plants and vertical bars represent the SE.

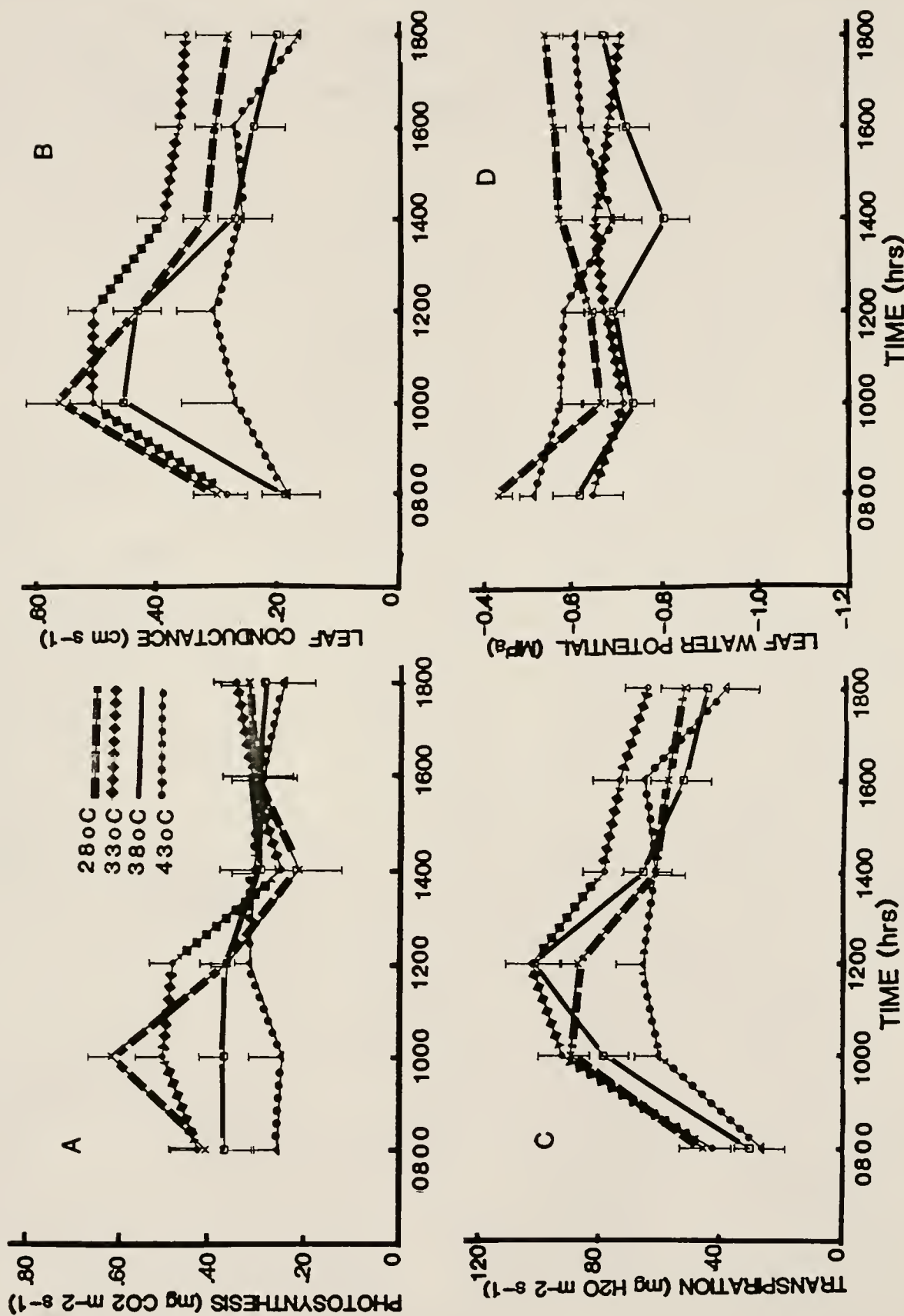
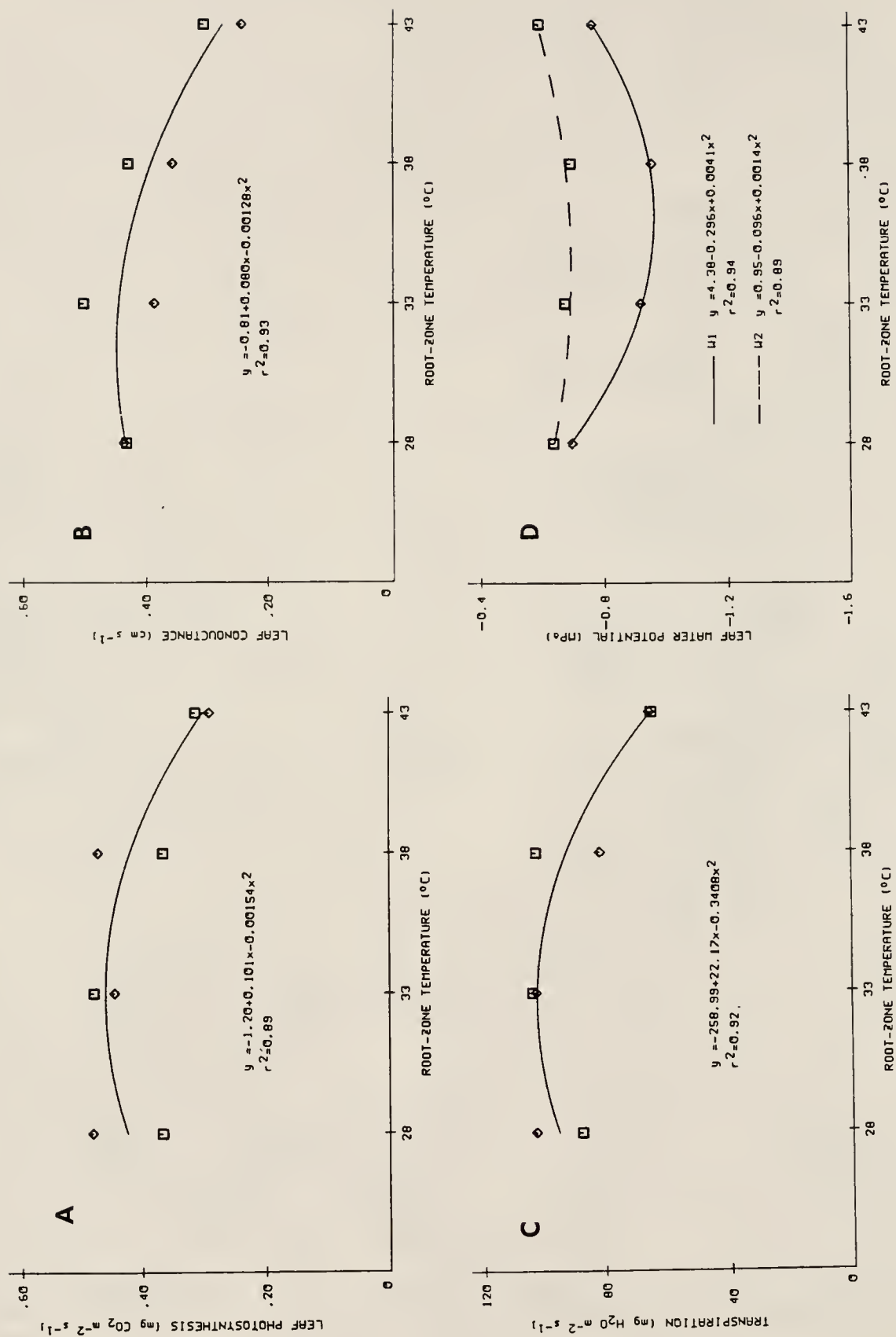


Figure 5-20. Regressions of midday physiological responses of container-grown *Ixora chinensis* L. 'Maui' over four root-zone temperatures and two irrigation volumes under growth room conditions. Main effects of root-zone temperature and irrigation volume on leaf photosynthesis, leaf conductance and transpiration are presented in A, B and C, respectively and interactive effects of root-zone temperature and irrigation volume on leaf water potential are presented in D. W1 (\diamond) = 75+8 ml, W2 (\square) = 150+15 ml daily per 1200 cm³ container.



inhibitory effects of the 43°C RZT on stomatal opening. The highest RZT however, appeared to limit root absorptive capacity as reflected by midday LWP, more in two-week old plants (Figure 3-3D) than at six weeks (Figure 5-18D).

The W2 irrigation volume treatment resulted in higher midday LWP for plants at the 33° and 38°C RZTs (Figure 5-20D). The W1 treatment apparently was inadequate for maintenance of good water status of plants at 33° and 38°C RZTs. While irrigation treatments significantly affected LWP, there were no apparent effects on the gas exchange processes. This discrepancy may have been due to the fact that while apical shoot sections were sampled for LWP measurements, recently matured leaves in ixora were selected for monitoring gas exchange data. In the 28°C RZT treated plants, there were not as many rapidly growing shoots as in higher RZT treated plants and this probably influenced LWP results at the 28°C RZT treatment.

Growth responses--ixora. Under growth room conditions, plant height and width were not influenced by stress treatments but axillary shoot number were greatest at the 33° and 38°C RZTs (Table 5-9). There were interactive effects of RZT and irrigation volume on axillary shoot length (Figure 5-21A). Shoot dry weight and thus shoot/root ratio increased curvilinearly with increasing RZT (Table 5-10) and RZT and irrigation interactive effects on total plant and root dry

Table 5-9. Growth components of *Ixora chinensis* L. 'Maui' measured after six weeks at four root-zone temperatures and two irrigation volumes under growth room conditions.

Stress treatments	Plant height (cm)	Plant width (cm)	No. of axillary shoots
RZT (°C)			
28	30.8	16.7	2.0
33	32.1	16.8	3.2
38	31.6	17.0	3.6
43	28.7	15.0	2.7
Irrigation volume (IRV)			
W1 ^z	30.2	16.3	2.8
W2	31.1	16.4	2.9
Significance ^y			
RZT	NS	NS	Q**
IRV	NS	NS	NS

^zW1 - 75±8 ml, W2 - 150±15 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Quadratic (Q).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

Table 5-10. Shoot dry weight, shoot/root ratio and chlorophyll concentration of *Ixora chinensis* L. 'Maui' measured after six weeks at four root-zone temperatures and two irrigation volumes under growth room conditions.

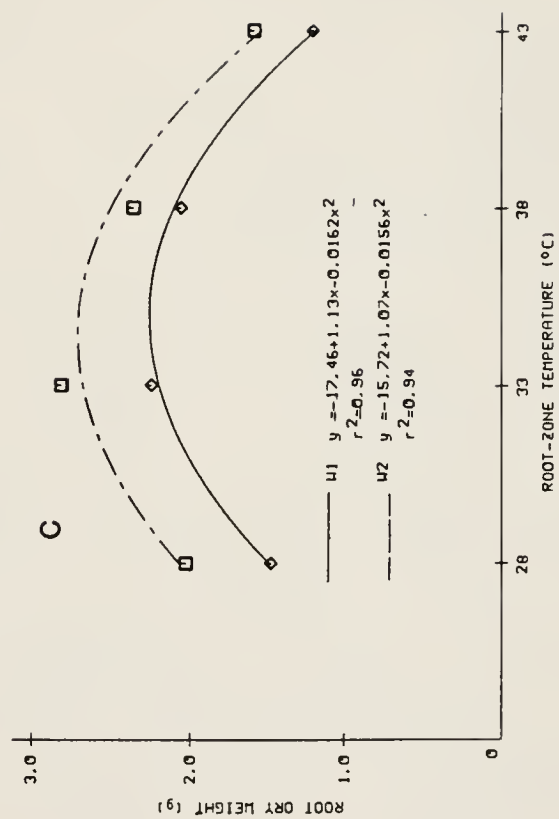
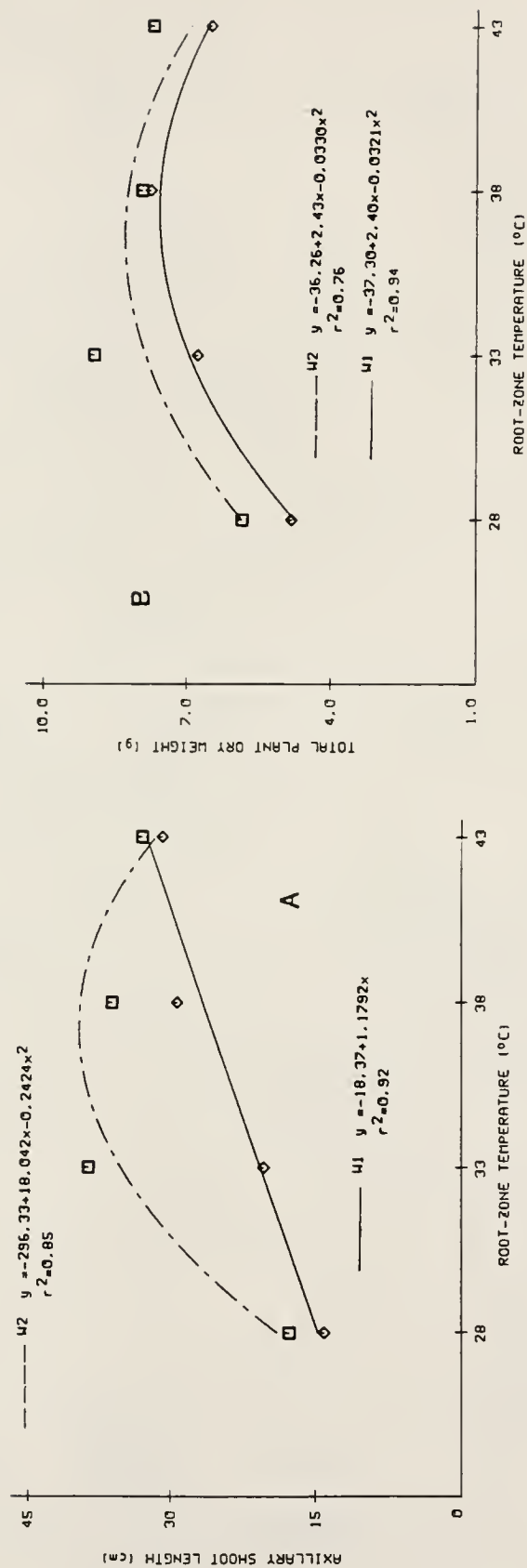
Stress treatments	Shoot dry wt (g)	Shoot/root ratio	Chlorophyll concn ($\mu\text{mol m}^{-2}$)
RZT ($^{\circ}\text{C}$)			
28	3.5	2.1	39.7
33	5.3	2.1	37.7
38	5.6	2.6	37.4
43	5.7	4.1	34.4
Irrigation volume (IRV)			
W1 ^z	4.7	2.9	37.2
W2	5.3	2.6	37.6
Significance ^y			
RZT	Q*	Q**	NS
IRV	NS	NS	NS

^zW1 - 75 \pm 8 ml, W2 - 150 \pm 15 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Quadratic (Q).

**, *, NS - significant at the 1%, and 5% probability levels and nonsignificant, respectively.

Figure 5-21. Effects of four root-zone temperatures and two irrigation volumes on growth of container-grown *Ixora chinensis* L. 'Maui' under growth room conditions. A. axillary shoot length B. total plant dry weight and C. root dry weight. W1 (◇) = 75+8 ml, W2 (□) = 150+15 ml daily per 1200 cm³ container. Points are irrigation treatment means.



weights were noted (Figure 5-21B, 5-21C). Stress treatments, however, did not influence relative chlorophyll concentrations (Table 5-10).

Stimulated axillary shoot length at 33° and 38°C RZTs was further augmented by increased irrigation (Figure 5-21A). Total plant (Figure 5-21B) and root (Figure 5-21C) dry weight parameters showed quadratic relationships with RZT, with the higher irrigation volume increasing dry weights at the 28° and 33°C RZTs. Apparently, the higher light intensity and/or longer photoperiod in the growth room retarded flowering in ixora compared to the greenhouse conditions. The lack of flowering prolonged apical dominance, particularly in the 28°C RZT treated plants. This resulted in an increased shoot number in plants exposed to RZTs above 28°C (Table 5-9).

The induction of axillary shoot growth at 33°C RZT has been implicated in studies by Franco (39) in coffee and Yusof (148) in avocado. Stimulation of branching and vegetative growth at the expense of flower production was reported for container-grown peppers (44) at RZTs above 36°C. Hormonal modification theories were suggested but not validated.

Carbohydrate analysis--ixora. Absolute shoot carbohydrate content was not altered by stress treatments but there were main effects of RZT on root sugar content and shoot sugar/root sugar ratio (Table 5-11). While root sugar content was maximum at 33° and 38°C RZTs, shoot sugar/root sugar was a minimum at these RZTs. These relationships

Table 5-11. Shoot and root carbohydrate distribution in Ixora chinensis L. 'Maui' after six weeks at four root-zone temperatures and two irrigation volumes under growth room conditions.

Stress treatments	Shoot sugar (% dwt)	Shoot starch (% dwt)	Root sugar (% dwt)	Root starch (% dwt)	<u>Shoot sugar</u> <u>root sugar</u>
RZT (°C)					
28	4.4	3.1	2.2	8.2	2.0
33	3.7	3.4	4.6	6.9	0.8
38	4.3	4.4	4.6	9.7	0.9
43	4.3	4.0	2.7	5.8	1.6
Irrigation volume (IRV)					
W1 ^z	4.3	3.6	3.5	7.9	1.3
W2	4.1	3.8	3.2	7.3	1.3
Significance ^y					
RZT	NS	NS	Q**	NS	Q**
IRV	NS	NS	NS	NS	NS

^zW1 - 75±8 ml, W2 - 150±15 ml per container daily.

^yStatistical differences between treatments resulting from orthogonal comparisons. Best fit models were Quadratic (Q).

**, NS - significant at the 1% probability level and nonsignificant, respectively.

indicated that although absolute shoot sugar content was unaffected by RZT, there was a tendency for increased translocation of sugars to the roots at the 33^o and 38^oC RZTs.

PS was generally higher in this study as compared to the greenhouse experiment, and although induced axillary shoot growth created extra sink demand, there probably was assimilate supply to satisfy the increase in shoot sink demand and that of the roots. Plants in the growth room did not flower and this may have reduced the demand for sugars in the shoots. The similarity in trends of root dry weight (Figure 5-21C) and root sugar content (Table 5-11) over RZT indicated that the supply of assimilate to the root was probably more than adequate for root growth at the 33^oC and 38^oC RZT. In vegetative rice (Oryza sativa L.), a 38^oC RZT increased the flow of ¹⁴C into the roots but decreased root dry weights were attributed to the reduced incorporation of carbon into protein and cell wall (97). In ixora under growth room conditions, increasing RZT to 38^oC apparently caused increased translocation of sugars to the roots and induced root growth. Environmental conditions appeared to highly influence the effects of RZT treatments on carbohydrate partitioning patterns.

CHAPTER VI SUMMARY AND IMPLICATIONS

The major objective of this project was to evaluate the effects of increasing RZT and irrigation volume, independently and in interactive studies, on container-grown 'Grande Naine' banana (Musa spp. AAA) and Ixora chinensis L. 'Maui.' A portable CO₂ gas analyzer system was used effectively to measure gas exchange processes simultaneously and the pressure chamber technique gave good indications of plant water status. The more controlled conditions of the walk-in growth room and the system of electronically controlled RHTs allowed for a more concise study of plant responses to RZT treatments than greenhouse conditions and air bath boxes. The use of tissue-cultured banana plants indicated that micropropagation can be an effective tool for investigating physiological responses to stress factors.

Experiments on the independent effects of irrigation volume reported in Chapter III showed conclusively that all physiological parameters in banana were decreased by decreasing irrigation volumes below the W3 (40±8 ml per 150 cm³ container daily; 85 to 100% CC) treatment. This parallels the results of most banana field research where physiological responses were reportedly disrupted by soil moisture levels below 66% ASM or 33% depletion of ASM (10,40,126).

Although gas exchange processes were reduced with decreasing irrigation levels, midday LWP in plants at W2 (20 ± 4 ml per 150 cm^3 container daily; 65 to 75% CC) were comparable to those at the W3 level. The morphological mechanism of lamina leaf folding, commonly seen in field plants at midday, was evident in the present study in plants that were water stressed to LWP of -0.51 to -0.65 MPa.

WUE has generally been quantified on a yield/evapotranspiration basis in banana field experiments (10,11) and though reported as leaf PS/leaf TR in this study, there was some parallel between the two interpretations. Plants in the greenhouse experiment grown under the W2 irrigation regime maintained PS with decreasing TR rates thus increasing photosynthetic WUE over the W3 treated plants. At the W1 irrigation level (10 ± 2 ml per 150 cm^3 container daily; 50 to 60% CC) plants could not effectively maintain any of the measured physiological processes. There was chlorophyll degradation as evidenced by leaf chlorosis and PS was severely reduced. Although not considered drought tolerant, the banana plant can apparently increase its photosynthetic WUE under declining irrigation.

Under growth room conditions, effects of irrigation volume on physiological responses were not as drastic as in the greenhouse experiment. At midday hours, plants under the W2 irrigation volume exhibited similar PS, CS and TR as those at the higher irrigation level. This increase in physiological responses at the W2 level was attributed mainly

to the effect of increased irradiance on stomatal opening and PS.

Progressive reductions in physiological parameters in ixora were also observed with decreasing irrigation volumes. WUE however, declined in parallel with decreasing irrigation levels and plants exhibited no apparent stress relieving mechanisms. In the drying cycle study, leaves wilted after irrigation was withheld for 4 days and abscised under further stress. Under growth room conditions, decreasing irrigation volumes did not affect physiological responses in ixora as severely as in the greenhouse and WUE decreases were also moderated.

Plant responses to RZTs of 28⁰, 33⁰, 38⁰ and 43⁰C imposed for 2 weeks were reported in Chapter IV. While the 33⁰C RZT induced maximum rates of gas exchange processes in banana under greenhouse conditions, plants grown in the growth room attained highest PS, CS and TR at the 38⁰C RZT. All parameters were reduced by the 43⁰C RZT under both environmental conditions. Most tissue-cultured banana plants are started in black polyethylene containers and RZTs above 33⁰C are commonly attained in such containers (59). Results from this study therefore indicate that nursery plants could be grown in such containers provided that media temperatures are limited to a maximum of 38⁰C.

An interesting comparison between RZT and water stress effects was initially observed in the short-term RZT banana experiments. Plant water status as reflected by LWP generally

declined with increasing RZT but plants did not exhibit leaf folding or show any chlorosis as exhibited in the directly water-stressed plants of the irrigation experiments. Some mechanism of conditioning or maintaining turgor under reduced LWP was theorized. In the subsequent long-term studies, carbohydrate analyses suggested that there may have been osmotic adjustment.

Measured physiological processes in ixora were not significantly different at RZTs of 28^o, 33^o and 38^oC but PS, CS and TR were reduced by the 43^oC RZT. PS at 38^o and 43^oC was decreased compared to the lower RZTs in the growth room experiment. This response of ixora to increasing RZT was generally similar to that exhibited in another rubiaceaeous genus, coffee (39), in which a RZT of 33^oC was reported to be optimum for growth and nutrient absorption.

In the final experiments, two irrigation volumes were factorially combined with four RZTs under greenhouse and growth room environments. Some interactions between RZT and irrigation volume occurred that could possibly be exploited in the container production of the two plants. Banana exhibited tolerance to increasing RZT up to 38^oC with significantly decreased rates in measured physiological responses induced by the 43^oC RZT in the greenhouse environment. Under growth room conditions, increased irrigation (150+15 ml per 1200 cm³ container daily; 90% to 100% CC) significantly increased midday PS in plants grown at a RZT of 33^oC. At 38^oC RZT, overall PS declined but increased

irrigation application had no effect. Stress effects induced by the 43°C RZT were moderated by increased irrigation in the high light condition of the growth room, but increased watering was actually detrimental to plants at the 43°C RZT in the greenhouse experiment. Root injury at the 43°C RZT probably caused reduced root absorptive capacity (118) and this was aggravated by the relatively small container volume in the greenhouse experiment.

The observed interactions could have important implications in the nursery phase of banana production. If growth medium temperatures are maintained at 33°C, increased irrigation would be beneficial. At a RZT of 38°C, overall PS would be reduced and increased irrigation would not alter this effect. Control measures would be essential if medium temperatures approached 43°C, since this RZT was shown to be supraoptimal under both environmental conditions investigated. Irrigation would need to be closely regulated since root injury caused by the 43°C could be aggravated by increased irrigation.

RZT stress was characterized morphologically by reduced leaf size in banana. A distinct decrease in leaf width but not leaf length or plant height was recorded in plants at the 38° and 43°C RZTs. A RZT-induced hormone mediated response associated with the loss of root tips at the high RZTs was postulated. This reducing effect on leaf area was not overcome by increased irrigation volume, indicating another interesting contrast between water and RZT stress effects.

The relatively small leaves at higher RZTs had increased chlorophyll concentration but this was not related to increased PS or shoot dry weight.

Carbohydrate analyses revealed significant differences in shoot/root and sugar/starch partitioning patterns. Comparison of the observed carbohydrate status with other physiological parameters suggested a possible role of sugars in allowing plants to maintain turgor under RZT-induced decreases in LWP. More detailed analyses, however, are needed to validate these theories and further interrelate RZT and water stress effects. The increase in stem diameter but not stem dry weight also supported the theory of increased plant turgor as one response to increased RZT. Because of the insignificant size of the corm in the plants under study, neither dry weight nor carbohydrate determinations were made of this tissue. This was one disadvantage of using banana plantlets in this study, since effects on the corm can influence final growth and yield performance of banana plants.

In the long-term study, carbohydrate partitioning in ixora appeared to be influenced by the RZT-induced axillary shoot growth and environmental conditions. New shoot growth represented an additional sink demand. However, because of the relatively low irradiance level and thus PS in the greenhouse, assimilates produced in the greenhouse-grown plants could not apparently supply both the additional shoot growth and the increased demands of roots at increasing RZTs.

This led to decreased root sugar content. Supply of assimilates in plants at the higher light level in the growth room environment was apparently adequate for both sinks and root sugar status was higher at the 33° and 38°C RZTs.

RZTs above 28°C caused increased axillary shoot growth in ixora. This finding is in agreement with similar effects of RZT in coffee (39), pepper (44) and avocado (148) but no direct physiological explanations for the increased shoot growth were reported. High air temperatures have also reportedly caused non-flowering orthotropic shoots in coffee (92) and a hormonal imbalance theory was postulated. The induced shoot growth in ixora influenced final growth parameters but was not accompanied by increased PS or TR. Increased vegetative growth was apparently at the expense of flowering and this led to the suggestion of a RZT-induced hormonal influence, possibly cytokinin, on plant growth and development.

Interactive effects of RZT and irrigation volumes observed in these studies could therefore have significant applications to the container phase of banana production schemes that convert to the tissue-culture method of propagation. Since ixora is used extensively as a floricultural landscape plant, container medium temperatures above 33°C in the nursery could have serious implications in its retail value.

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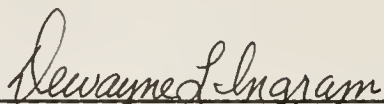
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BIOGRAPHICAL SKETCH


Christopher Ramcharan was born December 25, 1943, in Port-of-Spain, Trinidad. He attended Woodbrook Presbyterian Elementary School and St.Mary's College, Port-of-Spain, graduating in 1961. He entered the University of the West Indies, St.Augustine, Trinidad, in 1962 and graduated in July 1965 with the BSc in Tropical Agriculture. From 1965 to 1972 he was employed with the Department of Agriculture and served as Agricultural Officer at the Central Experiment Research Station, Centeno, and Superintendent of the Royal Botanic Gardens in Port-of-Spain, Trinidad.

In 1972, he was awarded a Trinidad and Tobago Government Development Scholarship which enabled him to enter the University of Florida and earn a MS degree in ornamental horticulture in December 1975. From 1978 he has been on the staff of the Virgin Islands Agriculture Experiment Station as research horticulturist. In August 1984 he re-entered the the University of Florida as a joint investigator of heat stress of tropical fruits and ornamental plants on a USDA Tropical Agriculture 406 Grant. During this time he also pursued graduate work towards the PhD degree in the area of root-zone temperature stress physiology.

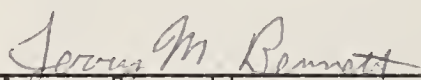
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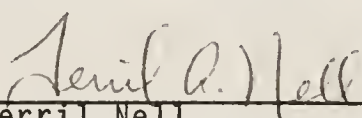
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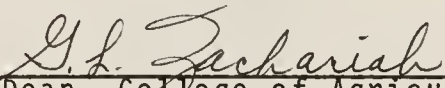
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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